

THE EVER-CHANGING LANDSCAPE OF CACTUS SYSTEMATICS¹

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ABSTRACT

Since Linnaeus originally described 22 species in the single genus *Cactus*, over 11,000 binomials and 400 generic names have been proposed for Cactaceae, and the nomenclature of cacti has been in a constant state of change and turmoil. When Engelmann began his cactus studies, only 25 generic names had been proposed, and the family was not well collected. Engelmann described and skillfully illustrated many cacti from the western United States and northernmost Mexico. By 1900, all known columnar species were classified in *Cereus* Miller; but soon Britton and Rose subdivided this form genus into many smaller and more homogeneous units. The descriptive phase of cactology has slowed, and since Buxbaum researchers have attempted to unravel the evolution of the family and to express phylogenetic information in a generic classification. One area of active phylogenetic research has been in tribe Pachycereeae, which includes the large columnar cacti of Mexico and adjacent areas. These species are often treated as two subtribes: Stenocereinae, which includes species with funicular pigment cells, abundant stem triterpenes, and seeds with verrucose testa having prominent striae; and Pachycereinae, which includes species that lack funicular pigment cells and that often have stem alkaloids but no triterpenes and seeds with smooth testa. New chemical surveys of Stenocereinae have revealed that an individual stem usually has a great number of triterpene glycosides and flavonoids. Crude visual comparisons are made of chromatographic patterns in triterpenes and flavonoids to evaluate existing phylogenetic hypotheses of the species groups. New reports of alkaloids in Pachycereinae are presented for *Lemaireocereus hollianus*, *Neobuxbaumia mezcalaensis*, *Pachycereus grandis*, and several species of *Cephalocereus*, but alkaloids are definitely absent in some of the species of *Cephalocereus* and *Neobuxbaumia* as well as *Mitrocereus*. In addition, alkaloids are reported here for the first time in species of Stenocereinae.

Cacti are famous for their beautiful flowers and many bizarre vegetative features, but they are equally famous—or infamous—for their nomenclatural and systematic problems, which are, indeed, formidable. Although most botanists are overwhelmed or greatly confused by the taxonomic literature on Cactaceae, some strides have been made to unravel the phylogeny of this family, which includes about 120 genera and 1,550 species (Gibson & Nobel, 1986). Moreover, systematic goals for cacti are no different than those met and addressed in any large and diverse family of plants: 1) to define the limits of each species; 2) to choose the oldest valid binomial; 3) to recognize monophyletic taxa; 4) to define the criteria to be used for erecting each genus; and 5) to produce a truly phylogenetic classification of the genera. This paper examines the problems of producing a phylogenetic classification for cactus genera. Following a brief review on the remarkable taxonomic legacy of Cactaceae, discussions will concentrate on the columnar cacti of tribe

Pachycereeae to demonstrate what types of research are needed to solve systematic problems in this family.

A BRIEF HISTORY OF CACTUS TAXONOMY

Christopher Columbus and his crew were undoubtedly the first Europeans to see cacti (Howard & Touw, 1981). Unfortunately, cacti were not mentioned in the published logs of the Columbus voyages (Morison, 1963), so this statement cannot be verified; but these explorers could not have missed cacti, which constitute a conspicuous part of the vegetation in the West Indies. Apparently the earliest New World description of cacti by a European was contributed by Oviedo (1526), who lived in the New World. Later Hernández (1514–1578) discussed 15 species of cacti in his famous account of Mexican plants that was eventually published in 1615.

By the 17th century cacti were already being cultivated in western Europe. Two unvalidated

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cactus names, “*Cereus Peruanus*” and “*Ficus Indica*,” appeared on a list of British plants by Gerard (1599). The earliest authentic report of *Melocactus communis* Link & Otto has been credited to Clusius in Holland, who in 1605 was brought a cultivated specimen from the island of Maio in the Cape Verde Islands near West Africa, where it was first spotted by Dutch seamen in 1601 (Heniger, 1973). How *Melocactus*, a New World genus, became established on Maio is a matter of speculation, but the Dutch were probably the ones who introduced this cactus from Curaçao, presumably in the mid or late 1500s. Bauhin and Cherler (1619; Bauhin, 1623; Rowley, 1976) mentioned the presence of species of “*Cereus*” and “*Ficus Indica*” in European gardens. Herbarium vouchers of *Opuntia* from the 1660s occur in the bound herbarium (*Hortus Siccus*, L) of Gaymans, a Leiden pharmacist, who documented the plants in Leiden’s Hortus Botanicus, the oldest botanical garden in The Netherlands. Many cactus species, including seven species of cereoids, were described from gardens in The Netherlands by Hermann (1687, 1698), and Boerhaave (1720) showed an engraving of the first flowering specimen (1 August 1691) of “*Cereus peruvianus*” in the Leiden botanical garden. Whatever role other countries had in introducing cacti to Europe is still unstudied, but certainly Dutch horticulturists were central in promoting the early interest in cactus cultivation, which soon became an avid passion of many gardeners.

The Dutch influence on cactus taxonomy extended, of course, to Linnaeus, who studied plants in The Netherlands. In *Hortus Cliffortianus*, which is a garden catalogue of the estate of Dr. George Clifford near Haarlem, Linnaeus (1737) mentioned 16 species in the genus *Cactus* and one species, which has large leaves, in the genus *Pereskia*. *Pereskia*, a name borrowed from the botanical illustrator Charles Plumier, honored Nicolas Claude Fabri, seigneur de Peiresc, who was a correspondent friend of Clusius. However, when Linnaeus (1753) published *Species Plantarum*, he classified all cacti in a single genus *Cactus*, with 22 species. Assigned to this taxon were platyopuntias, columnar cacti, epiphytes, barrel cacti, dwarf growth forms, and the leaf-bearing cacti. Subsequently, Miller (1754)⁵ recognized three additional genera, *Cereus*, *Opuntia*, and *Pereskia*, based on the earlier common

names, to emphasize some major differences in the cacti that were already known. At present, the species described by Linnaeus and Miller are classified in ten or more genera, belonging to three different subfamilies; since Linnaeus about 11,000 Latin binomials and an additional 400 generic names have been published for cacti. Regrettably, most published cactus binomials are illegitimate, invalid, or incorrect, because present-day cactus systematists recognize only 1,400–1,700 valid species and 70–140 genera. Moreover, in 1930, when *Mammillaria* Haworth was conserved, the name *Cactus* L. was declared a *nomen rejiciendum* because the lectotype of the family, *C. mammillaris* L., became a species of *Mammillaria* (Hunt, 1967; Shaw, 1976; Howard & Touw, 1981). Rejecting *Cactus* enabled taxonomists to resolve many nomenclatural problems and to reduce the ambiguity stemming from the inconsistent definitions and usage of *Cactus* by various authors.

Cacti described before 1820 were mostly species that were collected in the West Indies and along the eastern coastline of North and South America, such as from Brazil, Venezuela, Mexico, Florida, and Virginia. Some of the early discoveries were epiphytes, which were so remarkable in vegetative appearance and diversity that new generic names were proposed for the different forms, e.g., *Hariota* Adanson (1763), *Cassyta* J. Miller (1771), *Rhipsalis* Gaertner (1788), *Epiphyllum* Haworth (1812), *Phyllocactus* Link (1831), and *Lepismium* Pfeiffer (1835).

Taxonomic knowledge of Cactaceae accelerated rapidly when botanical exploration penetrated the arid and semiarid regions of the New World. New genera were proposed for low growth forms of Mexico: *Mammillaria* Haworth (1812), *Echinocactus* Link & Otto (1827), *Ariocarpus* Scheidweiler (1838), *Astrophytum* Lemaire (1839), *Echinofossulocactus* Lawrence (1841), and *Pelecypora* Ehrenberg (1843). Also, Pfeiffer (1838) proposed *Cephalocereus* as the first segregate genus of *Cereus*, based on the type, *Cactus senilis* Haw., an arborescent, solitary columnar cactus from Hidalgo, Mexico. Low growth forms collected in South America and the West Indies were assigned to other new genera: *Melocactus* Link & Otto (1827), *Echinopsis* Zuccarini (1837), *Discocactus* Pfeiffer (1837), and *Gymnocalycium* Pfeiffer (1845).

George Engelmann entered the field of cactus

⁵ Literature citations for all generic names mentioned in the following pages can be found in Hunt (1967).

taxonomy in the 1840s, after his reputation as a botanical taxonomist had already been established. Cactus materials collected in the United States and its territories were generally referred to him. Soule (1970), Mitich (1974), and Benson (1982) have written accounts of Engelmann's contributions to cactology between 1845 and 1878. During these years, Engelmann obtained live plants, herbarium specimens, first-hand descriptions, and illustrations of cacti from western North America and then reorganized, analyzed, and legitimately published names for hundreds of new taxa. Not all of Engelmann's names have survived careful systematic analysis, but it is a tribute to Engelmann that a great many of them are still considered correct.

The vast majority of common cacti of the southwestern United States and adjacent Mexico were first described by Engelmann, including seven of the ten cereoid species of the United States–Mexico borderland, 17 species and three varieties of cylindropuntias, about 20 species and varieties of platyopuntias, and over 50 species of the globular, caespitose, and barrel forms. Half of the binomials and trinomials accepted by Benson (1969a, 1969b, 1982) in the large cactus flora of California and Arizona have Engelmann as an authority, and Wiggins (1980) accepted 24 Engelmann taxa in Baja California, particularly species that occur in the northernmost latitudes. Specific epithets commemorate the people who collected specimens for his studies in St. Louis: *Ferocactus wislizenii* (Engelm.) Britt. & Rose, *Opuntia parryi* Engelm., *O. stanlyi* Engelm., *O. lindheimeri* Engelm., *O. bigelovii* Engelm., *Lophocereus schottii* (Engelm.) Britt. & Rose, *Stenocereus thurberi* (Engelm.) Buxb., *Peniocereus greggii* (Engelm.) Britt. & Rose, *Echinocereus fendleri* Engelm., and *Mammillaria wrightii* Engelm. Each taxon was very carefully described, and many were exquisitely illustrated by Paulus Roetter. Engelmann was also the person who proposed the genus *Echinocereus* (Engelmann, 1848), although he later changed his mind (Engelmann, 1849); and he recognized the distinctiveness of *Coryphantha*, which was later elevated to generic rank by Lemaire (1868).

Lemaire, who studied cacti during the same period as Engelmann, also made many individual contributions to cactus taxonomy for North and South America. He published 12 new generic names, at least six of which are still widely recognized (*Aporocactus*, *Cleistocactus*, *Schlumbergera*, and *Tephrocactus*, as well as the two Le-

maire genera already mentioned). At that time South American cacti were still relatively unknown, although Philippi (1860) reported new Chilean discoveries and described three distinctive genera, *Eriosyce*, *Eulychnia*, and *Maihuenia*. Cactus studies in arid and semiarid regions of North America were progressing through the floristic studies of Coulter, Orcutt, the Brandegees, and Weber. Weber also conducted cactus investigations on the Galápagos Archipelago and the epiphytic species of Costa Rica.

The taxonomic history of cacti was directed mostly by large descriptive monographs of the entire family, instead of by smaller monographs of individual genera. The first broad familial monograph was published at the turn of the century by Schumann (1898). Judged by today's standards, this classification is considered primitive, but Schumann made several interesting contributions. He was the first person to divide cacti into three subfamilies, which are still in use: Cereoideae, the largest taxon, which is now properly renamed Cactoideae in accordance with Article 19 of the International Code; Opuntioideae, which are the species having a white, bony aril covering the seed; and Peireskioideae (now spelled Pereskioideae), the large, relatively nonsucculent cacti that have large leaves (*Pereskia*) and the closely related *Maihuenia*, which are cushion plants (Gibson, 1977). Schumann recognized 21 genera, and he grouped the genera of Cactoideae into three tribes, Echinocactae (including the cereoids), Mamillarieae, and Rhipsalideae. These divisions were not phylogenetic in any modern sense. He rejected the name *Cactus* before it was proper to do so, and for the low growth forms he accepted many of the valid segregate genera that were mentioned above. Schumann ultimately proposed four new genera, *Zygocactus* (1890), *Rebutia* (1895), *Pterocactus* (1897), and *Wittia* (1903), but oddly enough he did not use either *Zygocactus* or *Rebutia* in his 1898 monograph; indeed, he did not even recognize *Rebutia* as a subgenus of *Echinocactus*, and he made *Zygocactus* a synonym of *Epiphyllum* Haw., which he and other cactologists totally misunderstood.

In 1904 Britton and Rose began their famous studies on the taxonomy of Cactaceae, which included a careful reexamination of all original descriptions and type specimens, extensive new field work in cactus areas throughout the New World, and assemblage of large living and dried collections for close study and photographing. Beginning in 1911, these studies were financed

by the Carnegie Institute of Washington, and Britton and Rose (1919–1923) eventually produced a four-volume taxonomic monograph, *The Cactaceae*, which is familiar to every systematic botanist and cactologist and is undoubtedly the most commonly cited and central cactus reference.

To discuss the contributions of Britton and Rose, some attention first must be paid to Berger, who was curator of the botanical gardens in La Mortola, Ventimiglia, Italy. Berger (1905) published a revision of the genus *Cereus* in which he recognized 18 subgenera. Many of these names were later used as genera by Britton and Rose but often in a much modified form. In Berger's revision, the columnar cacti that were known to him were those species that occurred in Mexico, the West Indies, Costa Rica, Peru, Chile, Argentina, and Brazil.

To assess fully the taxonomic contributions of Britton and Rose would take a very long article, half of which would consider the progressive, positive changes initiated by them, and half would analyze the errors in determination and judgment. Clearly, this familial monograph was and still is the cornerstone of cactus systematics. Britton and Rose accepted Schumann's three subdivisions, although they renamed these as tribes. In a massive revision of subfamily Cactoideae (Tribe Cereeae), Britton and Rose recognized 114 genera in eight subtribes and subdivided *Cereus* into many smaller and more homogeneous units. With this action, species of columnar cacti were placed into seven of the eight subtribes, and the name *Cereus* became restricted in usage to a small group of species in eastern and southern South America. Britton and Rose together described 77 new genera, and they published two more genera independently, *Harrisia* Britt. and *Escontria* Rose.

Looking at this great cactus monograph with 20–20 hindsight, it is easy to find many faults. One unfortunate choice was substituting *Neomammillaria* Britt. & Rose for *Mammillaria* Haw., which in 1930 was accepted internationally as a conserved name; this resulted in 186 unnecessary binomials under the new and ultimately illegitimate name. There were, of course, a number of genera that had improper membership, and binomials listed in synonymy have sometimes turned out to be "good" species that belonged in another genera. Moreover, at least 10 genera in the monograph appear now to be too narrowly defined to recognize, especially some

names that were proposed as segregates of *Mammillaria* and *Rhipsalis*. Regardless of this, at least 56 generic names of Britton and Rose (out of a total of 79) are widely regarded as sound taxa, although, as we shall discuss, some of these have been greatly redefined or are now being considered as subgenera. Consequently, the generic concept in cactus systematics often corresponds fairly closely to that presented by Britton and Rose.

Berger (1926) published an interesting book on the evolution of cactus genera, in which he used the Britton and Rose classification. Berger (1929) soon after published his own familial monograph, in which he accepted only 41 genera. He used 54 names authored by Britton and Rose but reduced these to subgeneric status. Overall, the classification scheme resembled that of Schumann, having three subfamilies, but in Cactoideae (as Cereoideae) he recognized only two tribes: Rhipsalideae, in which he included the rhipsaloid epiphytes plus *Epiphyllum*; and Cereeae, with four subtribes, in which he placed all other species of the subfamily. Consequently, the subtribal classification of Berger differed markedly from that of Britton and Rose.

Berger's 1929 classification system had many unusual and inconsistent features. For example, in "subsubtribus Echinocacteinae" the genus *Echinocactus* was very broadly defined, much like *Cereus*, and included barrel and small cacti from North and South America. However, in this subsubtribe he also included five monotypic Mexican genera, *Lophophora*, *Aztekium*, *Obregonia*, *Epithelantha*, and *Leuchtenbergia*, that are no less distinctive than some of the subgenera that he retained in *Echinocactus*. Likewise, in his subtribe Mamillarieae, Berger recognized 10 genera, of which six are no longer recognized; and in tribe Rhipsalideae he recognized six genera and many subgenera, most of which are not accepted now. Consequently, in this "conservative" classification, 13–15 of the 41 genera were more narrowly defined than most current cactus systematists would accept.

Cactologists universally acknowledged the great contribution of Britton and Rose, who were trained taxonomists. Bravo (1931, 1937) followed Britton and Rose in studies of the Mexican cacti, which are still being updated (Bravo, 1979); consequently, many collectors studying Mexican cacti have also followed Britton and Rose. Nonetheless, Schelle (1926) published a classification scheme that followed Berger (1905).

Working with a different generic concept were Frič, Backeberg, Ito, and other cactus horticulturists, who published many new generic names, more narrowly defined and often based on minor features. This new wave of classifications was stimulated first by the discoveries of new and exciting cacti in South America. Botanists and cactus growers began to collect extensively in the rich cactus areas of western South America. The plants that arrived in Europe from Ecuador, Bolivia, Peru, Chile, Uruguay, and Paraguay greatly changed the data base used by Britton and Rose to evaluate the South American genera.

The greatest source of new generic names was Backeberg. Slowly at first and then with a flourish, Backeberg (1958–1962, 1966) proposed many new genera and hundreds of species and varieties for South American materials. At the same time, he greatly subdivided and redistributed most of the Britton and Rose genera from the rest of the New World. In all about 81 generic names were published by Backeberg; however, today only 15–20 of these are still being considered seriously in taxonomic circles as useful taxa for a phylogenetic classification.

Backeberg was just one of several cactus horticulturists who increased the generic confusion of Cactaceae. For example, Frič published 52 new generic names, but of these only *Obregonia* has survived (Anderson & Skillman, 1984); and Ito proposed 18 new names, of which none have been widely accepted. Backeberg, Frič, Ito, and many other cactus enthusiasts were fascinated by variability of cacti, so they emphasized fairly minor and often plastic features in erecting new varieties, species, and genera. To be sure, commercial cactus businesses generally favored very liberal nomenclature to emphasize differences between plants. Nonetheless, there has been a backlash by numerous cactologists, both professional botanists and serious collectors, who have worked hard over the last 20 years to curb indiscriminate overnaming. Space limitations here do not permit a full review of the studies—published over the last 20 years—in which the number of species and genera has been carefully re-evaluated.

In North America the most remarkable part of this narrative unfolded. Cactus enthusiasts generally adopted Britton and Rose and began in earnest to define the species and varieties and to produce monophyletic genera. In contrast, Benson (1940) set out to study the cacti of the United States and Canada using the careful tech-

niques of Engelmann but the generic concept of Berger. Hence, in all cactus floras published by Benson (1969a, 1969b, 1970, 1982) and in floras and ecological studies that relied on Benson's monographs, such as the flora of Texas (Correll & Johnston, 1970), columnar cacti were classified in *Cereus* s.l. Benson (1969a) has briefly defended his reasons for using *Cereus*. From his viewpoint, "there is no 'right' or 'wrong' system" (p. 8), and a system should be one that conforms with the classification systems of other taxa and that is 'practical.' Benson felt that a conservative policy, i.e., placing all columnar forms in one genus *Cereus*, was in harmony with the overall conservative policy of plant systematics, and he also labeled the efforts of Britton and Rose as part of a "local 'liberalism'" that prevailed in the United States. He also felt that there are so few columnar cacti north of Mexico that it would be impractical to recognize so many monotypic genera for this area.

No other cactus taxonomist in recent history has agreed with Benson about the classification of columnar cacti. The reasons for this are many, but only two major points need to be discussed. First, the diversity of vegetative and reproductive features in columnar cacti is as great as the diversity of features present in low growth forms of North America, which Benson has recognized as distinct genera. Second, in order to understand and describe the phylogeny of the low growth forms in Cactoideae, which originated from columnar taxa, it is imperative to determine which part of the cereoid complex is the putative ancestor or sister taxon. The goal of modern cactus systematics, like that of the rest of plant systematics, is to make certain that each taxon above the species level is monophyletic in the strictest sense and reflects phylogeny.

Because none of the currently used classification systems for Cactaceae has been able to show that all taxa used are monophyletic, botanists can expect one more period in the history of cactus systematics in which traditional systems are studied intensively and rewritten to fit the modern guidelines for presenting phylogenetic hypotheses.

PACHYCEREEAE: AN EXAMPLE OF TAXONOMIC COMPLEXITIES

The Austrian botanist Franz Buxbaum deserves full credit for initiating a movement to develop a truly phylogenetic system of classifi-

cation for Cactaceae. He published many morphological papers on cacti (for a partial listing, see Gibson & Horak, 1978) during the same period that Backeberg was publishing his long list of segregate genera. The timing was unfortunate, because, in general, plant systematists were greatly distressed by the deluge of generic cactus names and paid little attention to new cactus publications, including the phylogenetic studies of Buxbaum. Although Buxbaum accepted a number of Backeberg names, he also studied the relationships of the species and provided excellent observations for rejecting many of Backeberg's conclusions.

Although Berger (1926) published on the generic relationships within Cactoideae, actually it was Buxbaum (1958) who proposed the first innovative phylogenetic classification of cactus genera and therein proposed most of the contemporary tribal names. Of these, Pachycereeae is the tribe that includes the large columnar cacti of Mexico and several other species that occur outside Mexico in the West Indies, Central America, and northern South America (Gibson & Horak, 1978; Bravo, 1979; Gibson, 1982). Buxbaum defined this tribe chiefly by listing the genera that he included in it. No synapomorphy currently defines this tribe in a strict cladistic sense; consequently, no one can categorically state which genera and species must be included. In the narrowest definition of the tribe, about 70 species would be included; there may be species in South and Central America that might be included but presently are not classified in this tribe. One derived feature that occurs in all species so far included is a wood skeleton composed of a ring of parallel, discrete, fastigiate rods (Gibson, 1978). A few columnar cacti in northern South America, e.g., *Neoraimondia*, have this design but are currently classified in tribe Leptocereae Buxb.

Tribe Pachycereeae can be effectively used as a model to show the systematic complexities of Cactaceae. Coincidentally, some of the species were first described by Engelmann, and even in his time there was a debate on generic names for columnar forms. In fact, numerous species of Pachycereeae have been transferred between genera, and a few have valid binomials in four or more genera. Another advantage of studying this tribe is that the alpha taxonomy of the Mexican species has been done (Bravo, 1979). To complement this, much structural and phytochemical data have been collected on these

species—more than in any other cactus tribe—which has enabled workers to attempt phylogenetic reconstructions using contemporary methods. Finally, phylogenetic modeling of this tribe is now in a new, third generation, so that older phylogenetic models can be tested to determine whether the original criteria still yield a parsimonious solution.

The taxonomic history of Pachycereeae began in 1753, when two West Indian species (*Cephalocereus* s.l.) were named by Linnaeus; however, the descriptions of columnar cacti from Mexico did not begin until the 19th century and then continued at a fairly steady pace until 1973, when *Stenocereus fricii* Sánchez Mejorada was described. Columnar cacti were initially described as species of *Cereus* or *Cactus*, but new combinations appeared when three segregate genera were proposed, *Cephalocereus* Pfeiff., *Cephalophorus* Lem., and *Pilocereus* Lem., which all cited the same type, *Cactus senilis* Haw. These segregates described what are broadly referred to as cephalocerei, fruticose and arborescent columnar cacti that have spineless flowers and fruits, relatively few bracts on the ovary and floral tube, and persistent and long, usually white hairs on the floriferous areoles.

The first species of Pachycereeae described by Engelmann was saguaro, *Cereus giganteus* (1848), and this was followed by organ pipe cactus, *Cereus thurberi* (1854), and senita, *Cereus schottii* (1856). In 1856 Engelmann described the subgenera *Lepidocereus*, *Eucereus*, *Pilocereus*, and *Echinocereus*. In subgenus *Lepidocereus* he included *C. giganteus* and *C. thurberi* of the Sonoran Desert along with *C. chilensis* Pfeiff. from South America. Subgenus *Pilocereus* included the cephalocerei; *Echinocereus* included the low, caespitose hedgehog cacti of North America; and *Eucereus* included other columnar forms. Two other species of columnar cacti from Mexico, *C. pecten-aboriginum* Engelm. and *C. gummosus* Engelm., were defined by Engelmann but were not published until after his death.

Lemaire recognized *Pilocereus*, in which he eventually placed all known cephalocerei as well as *C. schottii* and *C. giganteus*. *Pilocereus* was also accepted as a genus by Salm-Dyck, Weber, Rümpler, and Console, and it was used widely in horticultural circles. At the end of the century, Console proposed *Myrtillocactus* (1897) for *Cereus geometrizans* Mart., a distinctive, wide-ranging, arborescent cactus that produces two or more small, spineless flowers per areole. How-

TABLE 1. Classification of Pachycereeae into subgenera according to Berger (1905). Descriptions were abstracted from the key and diagnoses. After each species are listed the names used by Britton and Rose (1920) and Gibson and Horak (1978).

<i>Cephalocereus</i> (Pfeiff.) A. Berg. Flowers produced in a distinct cephalium; ribs with isolated mammillae that are surrounded by long hairs and spines; flowers small and arising singly from each mammilla.		
<i>Cereus chrysomallus</i> Hemsl.	<i>Pachycereus chrysomallus</i> (Lem.) Britt. & Rose	? <i>Backebergia militaris</i> (Audot) Bravo ex Sánchez Mejorada
<i>C. columna-trajani</i> Karw.	<i>Pachycereus columna-trajani</i> (Karw.) Britt. & Rose	<i>Cephalocereus hoppenstedtii</i> (Weber) K. Schum.
<i>C. macrocephalus</i> (Weber) A. Berg.	<i>Cephalocereus macrocephalus</i> (Haw.) Britt. & Rose	<i>Neobuxbaumia macrocephala</i> (Haw.) Buxb.
<i>C. melocactus</i> (Vell.) A. Berg.	<i>Cephalocereus fluminensis</i> (Miq.) Britt. & Rose	Unassigned
<i>C. senilis</i> DC.	<i>Cephalocereus senilis</i> (DC.) Pfeiff.	<i>Cephalocereus senilis</i>
<i>Lophocereus</i> A. Berg. Flowers several from each areole; flowering areoles differing from vegetative areoles by having numerous long setulose bristles; flowers reddish or yellowish; fruits scaly.		
<i>Cereus schottii</i> Engelm.	<i>Lophocereus schottii</i> (Engelm.) Britt. & Rose	<i>Lophocereus schottii</i>
? <i>C. scoparius</i> (Poselg.) A. Berg.	<i>Cephalocereus scoparius</i> (Poselg.) Britt. & Rose	<i>Neobuxbaumia scoparia</i> (Poselg.) Backeb.
? <i>C. urbanianus</i> (K. Schum.) A. Berg.	<i>Selenicereus urbanianus</i> (Gürke & Weing.) Britt. & Rose	Tribe Hylocereeae
<i>Myrtillocactus</i> (Cons.) A. Berg. Flowers very small, several per areole; ovary naked with a few minute scales; fruits small, smooth, reddish brown berries.		
<i>Cereus geometrizzans</i> (Mart.) Cons.	<i>Myrtillocactus geometrizzans</i> (Mart. in Pfeiff.) Cons.	<i>Myrtillocactus geometrizzans</i>
<i>Pachycereus</i> A. Berg. Flowers solitary, actinomorphic, tubular; ovary and tube covered with dense hair and thin bristles.		
<i>Cereus pringlei</i> S. Wats.	<i>Pachycereus pringlei</i> (S. Wats.) Britt. & Rose	<i>Pachycereus pringlei</i>
<i>C. pecten-aboriginum</i> Engelm.	<i>Pachycereus pecten-aboriginum</i> (Engelm. in S. Wats.) Britt. & Rose	<i>Pachycereus pecten-aboriginum</i>
<i>C. thurberi</i> Engelm.	<i>Lemaireocereus thurberi</i> (Engelm.) Britt. & Rose	<i>Stenocereus thurberi</i> (Engelm.) Buxb.
<i>C. fulviceps</i> (Weber) A. Berg.	<i>Pachycereus chrysomallus</i> (Lem.) Britt. & Rose	<i>Mitrocereus fulviceps</i> (Weber) Backeb. ex Bravo
<i>C. orcuttii</i> K. Brandeg.	<i>Pachycereus orcuttii</i> (K. Brandeg.) Britt. & Rose	× <i>Pachgerocereus orcuttii</i> (K. Brandeg.) Moran
<i>Lepidocereus</i> (Engelm.) A. Berg. Flowers solitary, actinomorphic, tubular, and large; greenish white; ovary with little short wool and sometimes a few deciduous bristles; fruits obovoid or pear-shaped with small and remote deltoid scales; plants very tall.		
<i>C. giganteus</i> Engelm.	<i>Carnegiea gigantea</i> (Engelm.) Britt. & Rose	<i>Carnegiea gigantea</i>
<i>Stenocereus</i> A. Berg. Flowers solitary, actinomorphic, tubular, small, and reddish or brown; ovary globose and with deltoid scales, naked, or with a few setulose hairs and little wool; fruit globose, brownish, and with a reddish pulp.		
<i>Cereus chiotilla</i> Weber	<i>Escontria chiotilla</i> (Weber) Rose	<i>Escontria chiotilla</i>
<i>C. dumortieri</i> Salm-Dyck	<i>Lemaireocereus dumortieri</i> (Scheidw.) Britt. & Rose	<i>Stenocereus dumortieri</i> (Scheidw.) Buxb.
? <i>C. marginatus</i> DC.	<i>Pachycereus marginatus</i> (DC.) Britt. & Rose	<i>Pachycereus marginatus</i>
<i>C. sonorensis</i> Rünge	<i>Rathbunia alamosensis</i> (Coult.) Britt. & Rose	<i>Stenocereus alamosensis</i> (Coult.) Gibson & Horak

TABLE 1. Continued.

<i>C. stellatus</i> Pfeiff.	<i>Lemaireocereus stellatus</i> (Pfeiff.) Britt. & Rose	<i>Stenocereus stellatus</i> (Pfeiff.) Riccob.
<i>C. alamosensis</i> Coult. (juvenile form of <i>C.</i> <i>stellatus</i>)	<i>Rathbunia alamosensis</i>	<i>Stenocereus alamosensis</i>
<i>C. aragonii</i> Weber	<i>Lemaireocereus aragonii</i> (Weber) Britt. & Rose	Unassigned
? <i>C. pruinus</i> Otto	<i>Lemaireocereus pruinus</i> (Otto) Britt. & Rose	<i>Stenocereus pruinus</i> (Otto) Buxb.
? <i>C. eburneus</i> Salm-Dyck	<i>Lemaireocereus griseus</i> (Haw.) Britt. & Rose	<i>Stenocereus griseus</i> (Haw.) Buxb.
? <i>C. resupinatus</i> Salm- Dyck	<i>Lemaireocereus griseus</i>	<i>Stenocereus griseus</i>
? <i>Pilocereus tetetzo</i> Weber	<i>Cephalocereus</i> ?	<i>Neobuxbaumia tetetzo</i> (Weber) Back- eb.
<i>Pilocereus</i> A. Berg. Flowers campanulate; ovary with very few scales and naked; fruit smooth and naked.		
<i>Cereus chrysacanthus</i> (Weber) A. Berg.	<i>Cephalocereus chrysacanthus</i> (We- ber) Britt. & Rose	<i>Cephalocereus chrysacanthus</i>
<i>C. exerens</i> Link	<i>Cephalocereus arrabidae</i> (Lem.) Britt. & Rose	Unassigned
<i>C. hermentianus</i> Monv.	<i>Cephalocereus hermentianus</i> (Monv.) Britt. & Rose	Unassigned
<i>C. hoppenstedtii</i> (Weber) A. Berg.	<i>Cephalocereus hoppenstedtii</i> (Weber) K. Schum.	<i>Cephalocereus hoppenstedtii</i>
<i>C. houlettii</i> (Lem.) A. Berg.	<i>Cephalocereus leucocephalus</i> (Po- selg.) Britt. & Rose	<i>Cephalocereus leucocephalus</i>
<i>C. lanuginosus</i> Mill.	<i>Cephalocereus lanuginosus</i> L.	Unassigned
<i>C. royeri</i> L.	<i>Cephalocereus royerii</i> (L.) Britt. & Rose	<i>Cephalocereus royerii</i>
<i>C. strictus</i> P. DC.	<i>Cephalocereus nobilis</i> (Haw.) Britt. & Rose	<i>Cephalocereus nobilis</i>
<i>C. ulei</i> (K. Schum.) A. Berg.	<i>Cephalocereus ulei</i> Gürke	Unassigned
<i>Eucereus</i> (Engelm.) A. Berg. Flowers large with a long and slender tube; ovary with numerous small deltoid scales; fruit more or less roundish and reddish, covered with spines that are often deciduous in clusters.		
Subsection <i>Nyctocereus</i> . Flowers nocturnal; stems more or less upright, cylindrical, and ribbed.		
<i>Cereus bivosus</i> Weber	<i>Lemaireocereus hollianus</i> (Weber) Britt. & Rose	<i>Pachycereus hollianus</i> (Weber) Buxb.
<i>C. candelabrum</i> Weber	<i>Lemaireocereus weberi</i> (Coult.) Britt. & Rose	<i>Pachycereus weberi</i> (Coult.) Backeb.
<i>C. cumengei</i> Weber	<i>Machaerocereus gummosus</i> (En- gelm.) Britt. & Rose	<i>Stenocereus gummosus</i> (Engelm.) Gibson & Horak
<i>C. eruca</i> Brandeg.	<i>Machaerocereus eruca</i> (Brandeg.) Britt. & Rose	<i>Stenocereus eruca</i> (Brandeg.) Gibson & Horak
<i>C. gummosus</i> Engelm.	<i>Machaerocereus gummosus</i>	<i>Stenocereus gummosus</i>
<i>C. queretaroensis</i> Weber	<i>Lemaireocereus queretaroensis</i> (We- ber) Saff.	<i>Stenocereus queretaroensis</i> (Weber) Buxb.

ever, according to Berger (1905), the segregate genera *Myrtillocactus* and *Pilocereus* were not accepted by professional botanists.

Table 1 shows how Berger (1905) classified into subgenera the species of Pachycereeae known

to him. Although Berger deserves credit for having the insight to search for subdivisions of the columnar cacti, it is easy to demonstrate now that his subgenera were often artificial. In subgenus *Cephalocereus*, Berger included five species

having "cephalia," four of which actually have pseudocephalia and which now belong to different genera. *Lophocereus* was created for *C. schottii* from the Sonoran Desert, which has multiple flowers from an areole that also produces long bristles, but included here by Berger was an unrelated species from Veracruz, Mexico, and another from the West Indies that is presently classified in tribe Hylocereeae. *Myrtillocactus* sensu Console was accepted as a subgenus, but Berger did not accept or discuss the taxon *C. cochal* Orcutt (1889) from Baja California. *Pachycereus* included species with dense wool and golden bristles on the fruit, but this subgenus also included *C. thurberi* Engelm., which does not fit the description of the subgenus. *Stenocereus* was Berger's most interesting taxon and included many species that are closely related, but the diagnosis of this subgenus was inaccurate. For example, the flowers of *Stenocereus pruinosus* are not small, but rather are 9 cm or more in length; moreover, the flowers of *Escontria chiotilla* have bright yellow petals, not reddish or brown, and the pulp of its fruit is purplish, not reddish. In addition, fruits of *Lemaireocereus aragonii* have a white pulp and those of *Stenocereus dumortieri* have a pulp that is essentially colorless. *Pilocereus* was used in the same sense as Lemaire's except that the type, *C. senilis*, was excluded and placed in subgenus *Cephalocereus*. Finally, Berger combined species having flowers with nocturnal anthesis in subsection *Nyctocereus* in subgenus *Eucereus*.

After Berger published his 1905 version of *Cereus*, Britton and Rose studied columnar cacti and decided to recognize additional genera for the Mexican pachycereine species. The largest genus accepted was *Cephalocereus*, which they interpreted in the comprehensive sense of Lemaire's *Pilocereus*, i.e., all species with spineless reproductive structures and long hairs on the floriferous areoles. Consequently, this genus included species from South America. *Myrtillocactus* was adopted, and the monotype *Escontria* Rose (1906) was proposed for the only species in Mexico with large, translucent, chartaceous bracts covering the flowers and fruit. The generic name *Carnegiea* was proposed to replace subgenus *Lepidocereus*; this substitution eliminated the need to use the polyphyletic taxon of Engelman and also permitted Britton and Rose to honor the Carnegie Institute for supporting cactus and desert research.

In a landmark taxonomic paper, Britton and

Rose (1909) proposed four more genera. *Lophocereus* was raised to generic rank but was reduced from three species in Berger's system to one, *L. schottii*. *Pachycereus* became a genus similar to the Berger subgenus and was based on the presence of bristles on the fruit. The name *Lemaireocereus* was proposed to include Mexican species that have fruits and sometimes flowers with spine clusters. Species of *Lemaireocereus* were pulled from several subgenera of Berger (Table 1), especially *Stenocereus* and *Eucereus*. Two species with short, tubular, slightly zygomorphic red flowers were also segregated as the genus *Rathbunia*. Britton and Rose (1919–1923) recognized nine genera because they removed two species from *Lemaireocereus* to create *Machaerocereus*, *M. gummosus* (Engelm.) Britt. & Rose, and *M. eruca* (Brandeg.) Britt. & Rose from Baja California, which have nocturnal anthesis and heavy central spines.

About one month after Britton and Rose published their first major generic monograph, Riccobono in 1909 made an important contribution when he proposed the name *Stenocereus stellatus* (Pfeiff.) Riccob., which was based on subgenus *Stenocereus* of Berger (1905). *Stenocereus stellatus* was an excellent choice for type because it has all of the important features of the stenocerei.

Since Britton and Rose, over 20 generic names have been proposed for the pachycereine plants. Most of these names were added by Backeberg, and these were often defined so narrowly that most had only one or a few species. Consequently, there existed a great need to determine the phylogenetic relationships of the species so that generic decisions could be solidified.

PHYLOGENETIC STUDIES OF BUXBAUM

When Buxbaum (1958) proposed his first phylogenetic hypothesis for Cactoideae, in tribe Pachycereeae Buxb. he accepted six genera, *Pachycereus* Britt. & Rose, *Lemaireocereus* Britt. & Rose, *Neobuxbaumia* Backeb., *Carnegiea* Britt. & Rose, *Cephalocereus*, and *Mitrocereus* Backeb., with *Escontria* Rose and *Anisocereus* Backeb. listed as "genera incertae sedis." He adopted *Pachycereus*, *Lemaireocereus*, and *Cephalocereus* of Britton and Rose with some important deletions: *Mitrocereus* was a taxon removed from *Pachycereus* and split into two species; *Neobuxbaumia* consisted of some species that had been scattered throughout *Cephalocereus* by past authors; and *Austrocephalocereus* Backeb. consist-

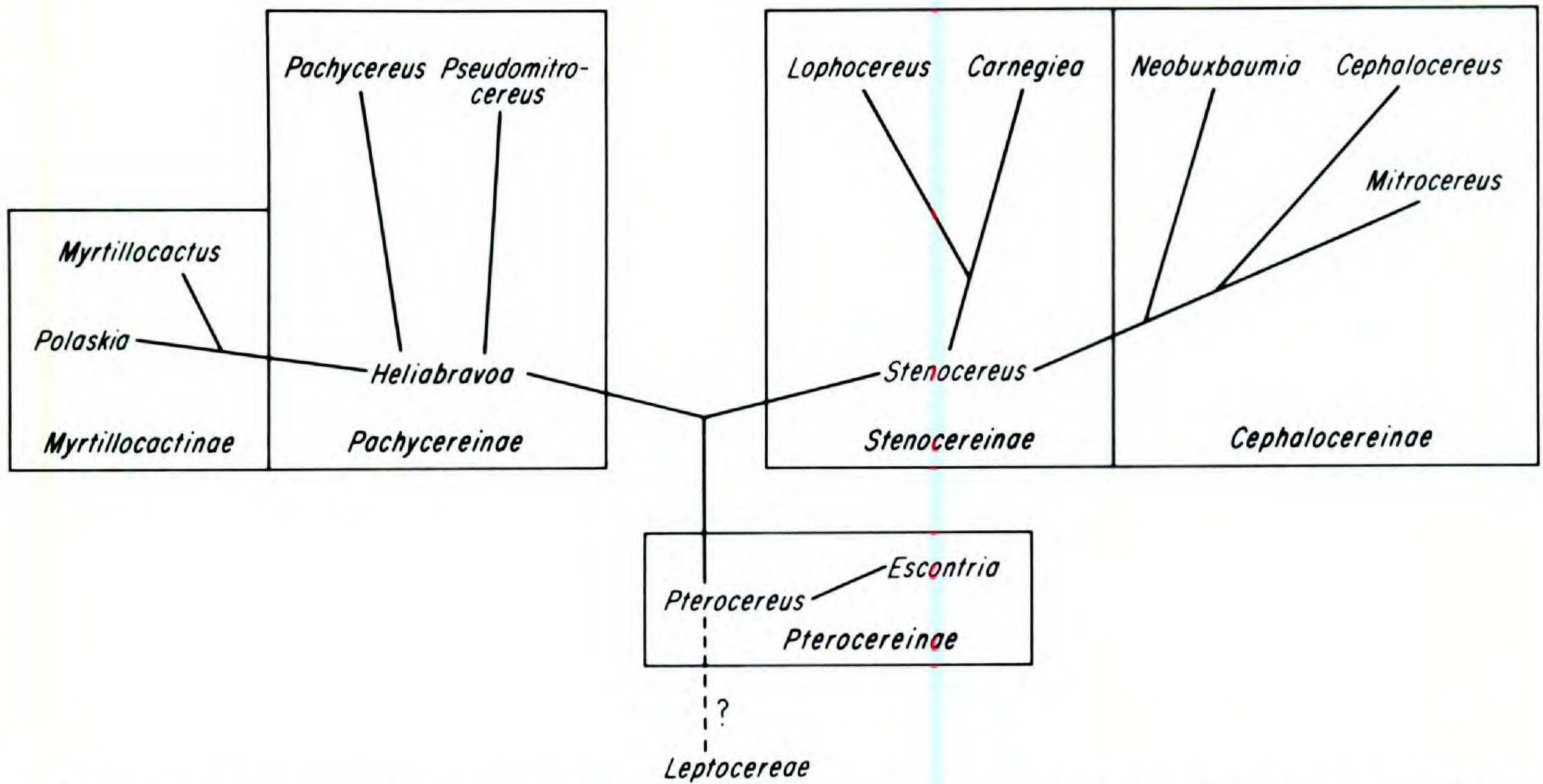


FIGURE 1. The first phylogenetic model of Pachycereeae by Buxbaum (1961), in which he recognized five subtribes and proposed Leptocereae as the putative ancestor.

ed of South American cephalocerei and was removed to tribe Cereeae Buxb.

Three years later Buxbaum (1961) presented a greatly modified interpretation of Pachycereeae. For its time, this was a remarkably detailed phylogenetic paper on a cactus tribe. Buxbaum recognized 13 genera, and of these only *Neobuxbaumia* and *Carnegiea* were unchanged. *Lemaireocereus* was reduced in size by removal of certain non-Mexican species for reassignment in *Armatocereus* Backeb. of tribe Leptocereae; by recognition of two monospecific genera, *Heliabravoa* Backeb. and *Polaskia* Backeb., from southern Mexico; and by exchanging several species between *Lemaireocereus* and *Pachycereus* sensu Britton and Rose. At that time *L. hollianus* (Weber) Britt. & Rose, the type, was transferred into *Pachycereus*, which required the adoption of the name *Stenocereus* for the species left in "*Lemaireocereus*." Three-ribbed species were removed from *Pachycereus* to become the segregate *Pterocereus* Backeb.; and *Anisocereus lepidanthus* (Eichl.) Backeb., which was formerly a species of *Pachycereus*, was added to *Escontria*. *Mitrocereus*, which originally consisted of two species, was treated as two distinct, monospecific genera, *Mitrocereus* and *Pseudomitrocereus* Bravo & Buxb., which later were renamed *Backebergia* Bravo and *Mitrocereus*, respectively (Sánchez Mejorada, 1973b). In addition, Buxbaum transferred *Lophocereus* Britt. & Rose and *Myrtillocactus* to Pachycereeae from tribe Cereeae.

Hence, this tribe began to be redefined as a Mexican taxon with some outliers in the neighboring countries and the West Indies.

Buxbaum described and illustrated the flowers, fruits, seeds, and seedlings more carefully than most previous workers, and he discovered some features that were exceedingly important in analyzing their phylogenetic relationships. First, he documented seed structure for many species, generally magnified 10–30 times, revealing testal features. He also discovered that at anthesis some species of Pachycereeae had idioblastic pigment cells in the funicular epidermis, which subsequently develop into spherical pigment cells in the fruit pulp. He termed these structures "pearl cells" (Perlzellen) because they appeared as colored beads on a colorless string (funiculus). Moreover, Buxbaum was keenly interested in the presence of triterpenes in some of these species, which had been biochemically investigated by Djerassi (1957; Gibson & Horak, 1978).

Buxbaum's first phylogenetic diagram of Pachycereeae (Fig. 1), which arranged the genera into five subtribes, differed in no substantial way from even the final version (Gibson & Horak, 1978), except that he eventually combined subtribes Stenocereinae and Cephalocereinae to form a larger Stenocereinae and also added *Machaerocereus* Britt. & Rose (Buxbaum, 1968) and *Rathbunia* Britt. & Rose (Buxbaum, 1975) to this subtribe as derivatives of *Stenocereus* (A. Berger)

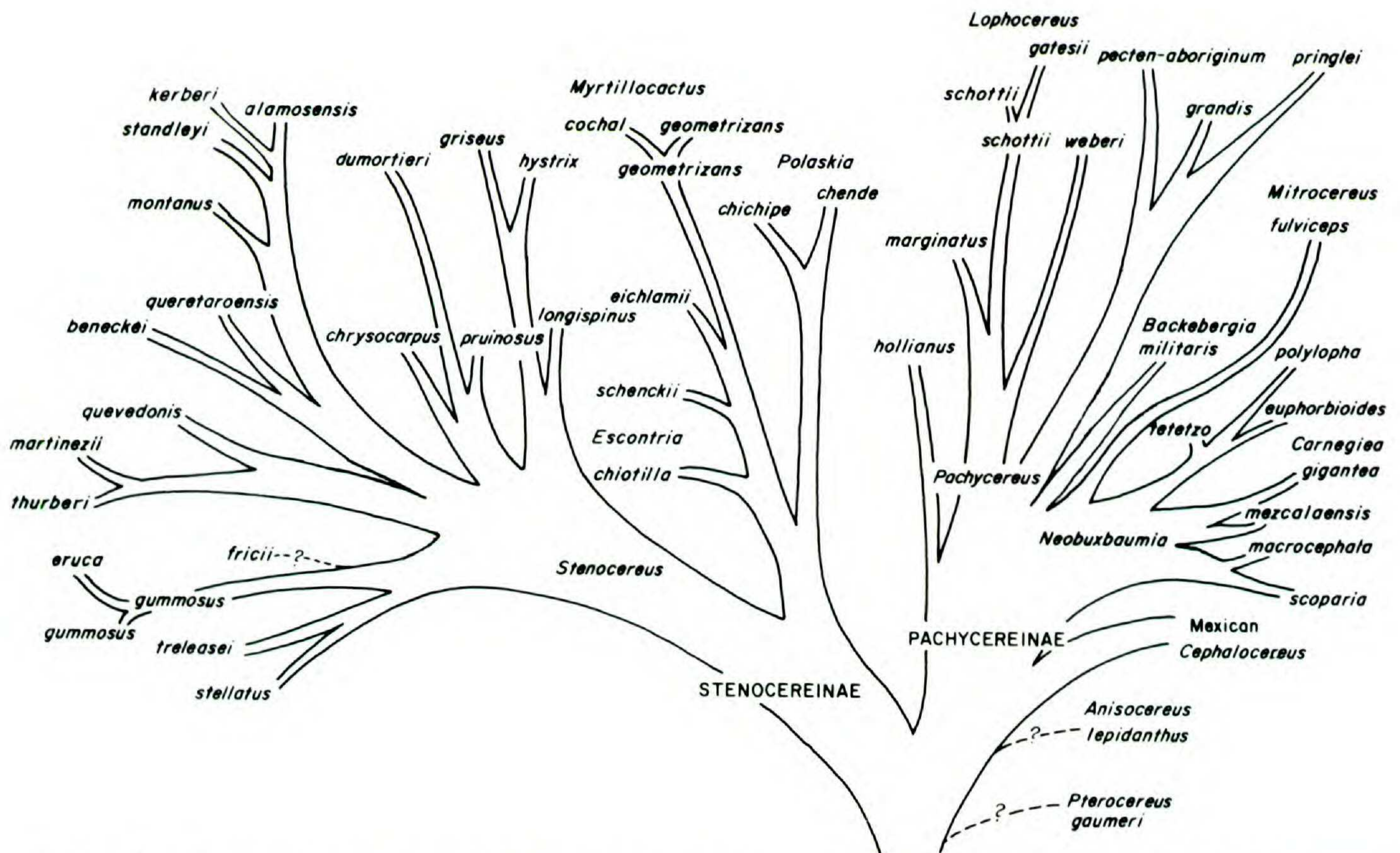


FIGURE 2. The original phylogenetic hypothesis of Pachycereaceae by Gibson and Horak (1978), which recognized two major subtribes, Stenocereinae and Pachycereinae.

Riccob. Interestingly, Buxbaum used the presence of funicular pigment cells and of stem triterpenes as the chief criteria for including these two genera in Pachycereaceae.

TESTING BUXBAUM'S MODEL

For many years population biologists have studied the evolutionary genetics and ecology of *Drosophila* living in rotting tissues of cacti, especially in the columnar cacti of the Sonoran Desert (Barker & Starmer, 1982). Some species of cactophilic *Drosophila* are host-specific, whereas others are found on several or many species of cacti. In 1974, the *Drosophila* scientists requested assistance from the senior author for information on the phylogenetic relationships of *Drosophila* host plants in Pachycereaceae; consequently, the phylogenetic model of Buxbaum was examined.

None of the patterns in *Drosophila* speciation, host-plant preference, or host-plant chemistry could be logically explained by the phylogenetic model; consequently, a study was initiated to test the overall validity of Buxbaum's phylogenetic model for Pachycereaceae. To do this, species lists were prepared from the literature for selected derived characteristics, such as glycosidic triterpenes (23 species), pearl cells (13 species), and

alkaloids (6 species), and these were tested against the existing phylogeny for congruence. Three observations were made. (1) Buxbaum's model failed tests of parsimony for these sets of data. For example, in his model, species with abundant triterpenes were portrayed as derivatives of species with abundant alkaloids, and vice versa. (2) Species known to have abundant glycosidic triterpenes seemed to lack alkaloids, and those with abundant alkaloids generally lacked triterpenes. (3) All species known to have pearl cells also had abundant glycosidic triterpenes. Because there was no apparent biological link between the specialized pigment cells in the locule and colorless stem triterpenes, the coincidence of two apomorphic features in a group of species suggested that these species belong to a monophyletic taxon and that realignments would be required.

To aid in the production of new phylogenetic hypotheses, stem transections were studied from the majority of species in Pachycereaceae as well as in some columnar species from other tribes. Gibson and Horak (1978) discovered silica bodies in the skin (epidermis plus hypodermis) of some Pachycereaceae. Silica bodies are uncommon in plants and were previously unreported from Cactaceae, and in Pachycereaceae they occurred only in species with abundant glycosidic triter-

penes (oleanane class) and pearl cells. Conversely, a different set of species in Pachycereeae that lacked pearl cells had prismatic crystals of calcium oxalate in the skin. Using these synapomorphies, combined with general data on plant morphology, anatomy, and chemistry, a new phylogenetic model was proposed (Fig. 2). Species having or thought to have abundant oleanane triterpenes and pearl cells were classified as subtribe Stenocereinae, whereas any taxon with calcium oxalate crystals or abundant stem alkaloids was classified in subtribe Pachycereinae.

In Stenocereinae sensu Gibson and Horak, all species possessing silica bodies were reclassified in the emended genus *Stenocereus*, including *Machaerocereus* and *Rathbunia* as well as the Backeberg segregates *Hertrichocereus*, *Isolotocereus*, *Marshallocereus*, *Neolemaireocereus*, and *Ritterocereus*. When *Lemaireocereus hollianus* was moved out of subtribe Stenocereinae, because it lacked the synapomorphic features, Gibson and Horak (1978) followed Buxbaum (1961) in recognizing this as a species of *Pachycereus*. Also included in subtribe Stenocereinae was *Myrtillocactus*, *Escontria* s.s. (excl. *Anisocereus lepidanthus*), and *Polaskia*, which was combined with the monotype *Heliabravoia*.

In Pachycereinae, all of the genera recognized by Buxbaum were retained (*Lophocereus*, *Pachycereus*, *Backebergia*, *Cephalocereus*, *Carnegiea*, *Mitrocereus*, and *Neobuxbaumia*), but the genera were clustered to explain the occurrence of synapomorphic structural features. Two species of *Pachycereus*, *P. marginatus* (DC.) Britt. & Rose (= *Marginatocereus* Backeb.) and *P. weberi* (Coul.) Backeb., had been classified by many authors as either species of *Lemaireocereus* or *Stenocereus*; but because they have abundant alkaloids and lack pearl cells, they were removed from Stenocereinae. *Pterocereus* and *Anisocereus* were placed at the base of the phylogenetic tree (Fig. 2) without defining precisely how these are related to the two subtribes.

Gibson and Horak (1978) speculated on the proposed phylogenetic relationships of the species. Briefly, they suggested that speciation of these cacti fit an allopatric model, i.e., geographic speciation, in which the northern cacti, located in the Sonoran Desert, are the most highly derived and probably relatively recent species of seven different clades. Moreover, these cacti have many different floral designs that are adapted to use different types of pollinators, so that very closely related species often differ markedly in

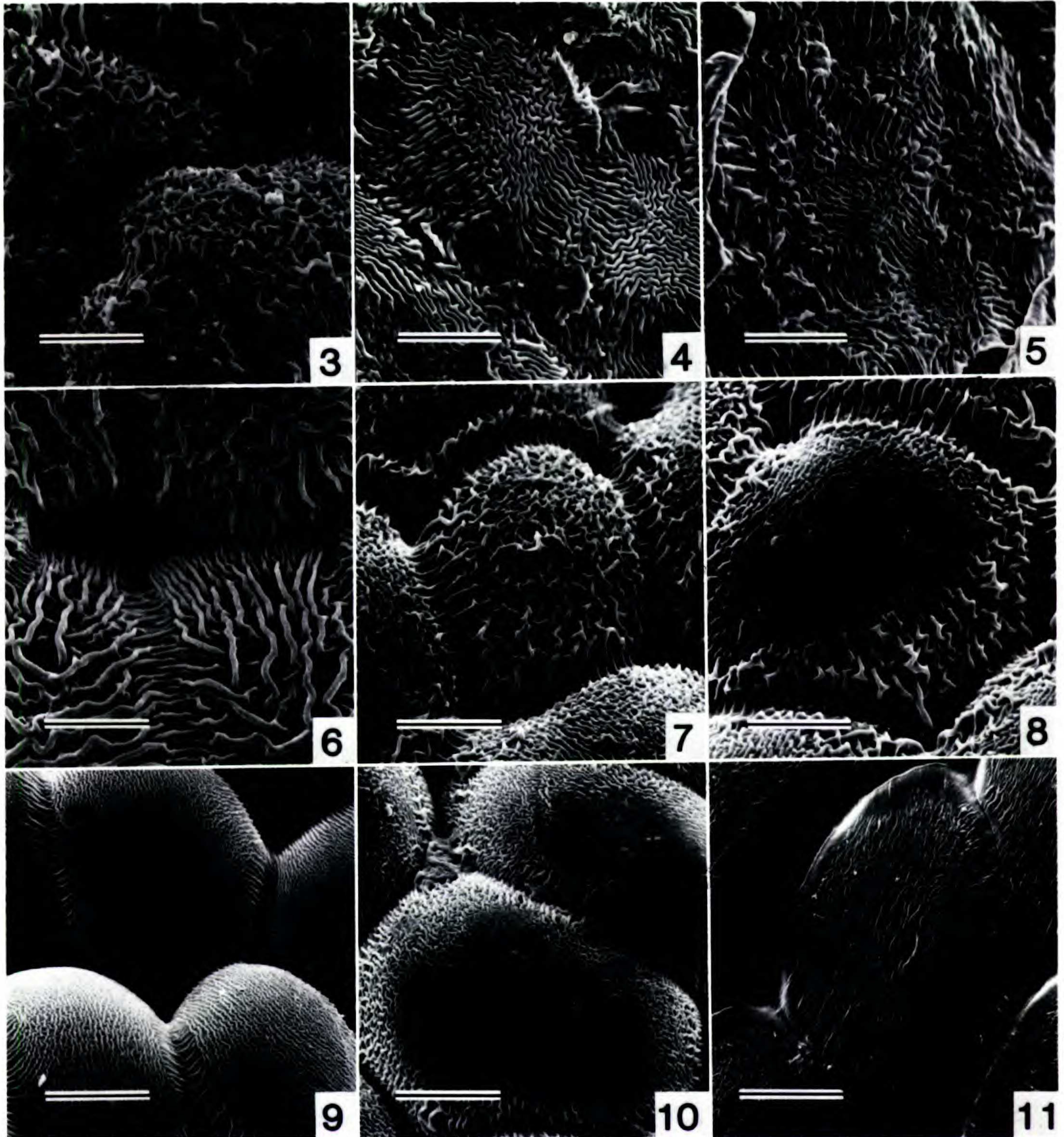
flower shape, length, color, position, and time of anthesis. The plethora of generic names in this tribe has resulted in part because previous authors emphasized the importance of external floral features for identifying taxa.

RECENT INVESTIGATIONS OF PACHYCEREEAE

Although Gibson and Horak (1978) were able to provide a fairly clear justification for reorganizing the species into monophyletic genera, the evidence for circumscribing subtribes, genera, and intrageneric groups was, to be sure, weak and incomplete. Any contemporary phylogeneticist viewing Figure 2, which was drawn in 1976, can see that this is not a precise statement of phylogenetic relationships of the species, especially in *Stenocereus*. Beginning in 1980, new vegetative and reproductive materials of Pachycereeae were collected in the field for structural and chemical analyses, with the goal that a cladistic model of the genera and species eventually could be produced. As new data were collected, some of the conclusions of Gibson and Horak were strongly reinforced, whereas others were clearly wrong or misguided and had to be discarded or modified.

Seed ultrastructure. The seeds of Pachycereeae were collected and examined with a scanning electron microscope to document testal sculpturing. Because data on seeds were very uneven and incomplete in Gibson and Horak (1978), a thorough study of seed ultrastructure was the first broad test of their phylogenetic model. *Lemaireocereus* sensu Britton and Rose (1920) exhibited a wide diversity of seed types, ranging from 4 mm to less than 0.5 mm long, brown to black, rough to smooth, and dull to glossy. As reconstituted, subtribe Stenocereinae Buxb. emend. Gibson & Horak basically included those species with relatively small, dull, rough seeds, called verrucose in recent accounts. However, the subtribe seemed to include several noteworthy exceptions.

Seeds of 22 species and one variety of the 30 species in subtribe Stenocereinae were analyzed, including any species whose seed morphology was not noticeably verrucose. Figures 3–11 show that all four genera have seeds characterized by convex cells with convex outer walls that have prominent cuticular striae, and the striae tend to traverse the cell margins (Figs. 3–9). This testal design was previously found in Pachycereeae by Leuenberger (1974) and Barthlott and Voit (1979)



FIGURES 3–11. Scanning electron photomicrographs of testa of Stenocereinae, showing characteristic cuticular striae.—3. *Escontria chiotilla* (Weber) Rose, *Gibson 3731* (RSA). Bar = 0.1 mm.—4. *Polaskia chende* (Gossel.) Gibson & Horak, *Gibson 3180* (ARIZ). Bar = 0.2 mm.—5. *Myrtillocactus geometrizans* (Mart.) Cons., *Gibson 3754* (RSA). Bar = 0.2 mm.—6. *Polaskia chichipe* (Gossel.) Backeb., *Gibson 3734* (RSA). Bar = 0.2 mm.—7. *Stenocereus pruinosus* (Otto) Buxb., *Gibson 3729* (RSA). Bar = 0.2 mm.—8. *Stenocereus pruinosus*; same seed as but different region than Figure 7, showing that cell size and prominence of striae varies considerably. Bar = 0.2 mm.—9. *Stenocereus quevedonis* (G. Ortega) Buxb., *Gibson 3713* (RSA). Bar = 0.2 mm.—10. *Stenocereus chrysocarpus* Sánchez Mejorada, *Gibson 3716* (RSA). Bar = 0.2 mm.—11. *Stenocereus thurberi* (Engelm.) Buxb., *Gibson 3751* (liquid-preserved voucher). Bar = 0.2 mm.

and is fairly widespread in Cactoideae (Barthlott & Voit, 1979; Barthlott, 1981; Behnke & Barthlott, 1983). On the very small seeds of *Myrtillocactus* and *Polaskia chende* (Gossel.) Gibson & Horak (Figs. 4–5), striae are fairly low but are

still quite evident; and in some species of *Stenocereus*, the striae in the center of each cell may be reduced so that the surface appears fairly smooth. In *Stenocereus thurberi*, which superficially appears to have smooth, black seeds, the

testal cells are somewhat flattened but still retain striae (Fig. 11). In *S. alamosensis* (Coul.) Gibson & Horak (Fig. 12) the seed coat is very smooth except between the cells, where faint striae can be observed to cross the cell margins. Once again, the closely related species *S. kerberi* (Schum.) Gibson & Horak and *S. standleyi* (G. Ortega) Buxb. have typical seed features of *Stenocereus*. Finally, in *S. beneckeii* (Ehrenb.) A. Berger & Buxb. (Fig. 13), which has the largest seeds in the subtribe (3 mm) and the thickest testa, the testa lacks well developed rugae and striae but is still quite rough. *Stenocereus beneckeii* has the vast majority of features found in the genus, including silica bodies, abundant triterpenes, and red areolar trichomes but no pearl cells. Each of these deviations from the standard testal design of Stenocereinae can be explained as a secondary modification.

In species assigned to Pachycereinae, none of the seeds are dull or rough. On these seeds (Figs. 14–20), the cuticle is smooth, and the cells bulge outward only slightly or are flat. In some species of *Pachycereus*, the outlines of the cells are difficult to distinguish (Figs. 15–20); but in *P. marginatus* (Fig. 15) and *P. weberi* (Fig. 16), deep pits form at the cell corners. Only in certain species of *Cephalocereus* have striae been observed traversing the cell margins, in a manner similar to *S. alamosensis*. There does not seem to be a single seed type or testal design characteristic of all Pachycereae as presently defined, and especially the seed of *Pachycereus hollianus* (Fig. 20) is atypical of the subtribe.

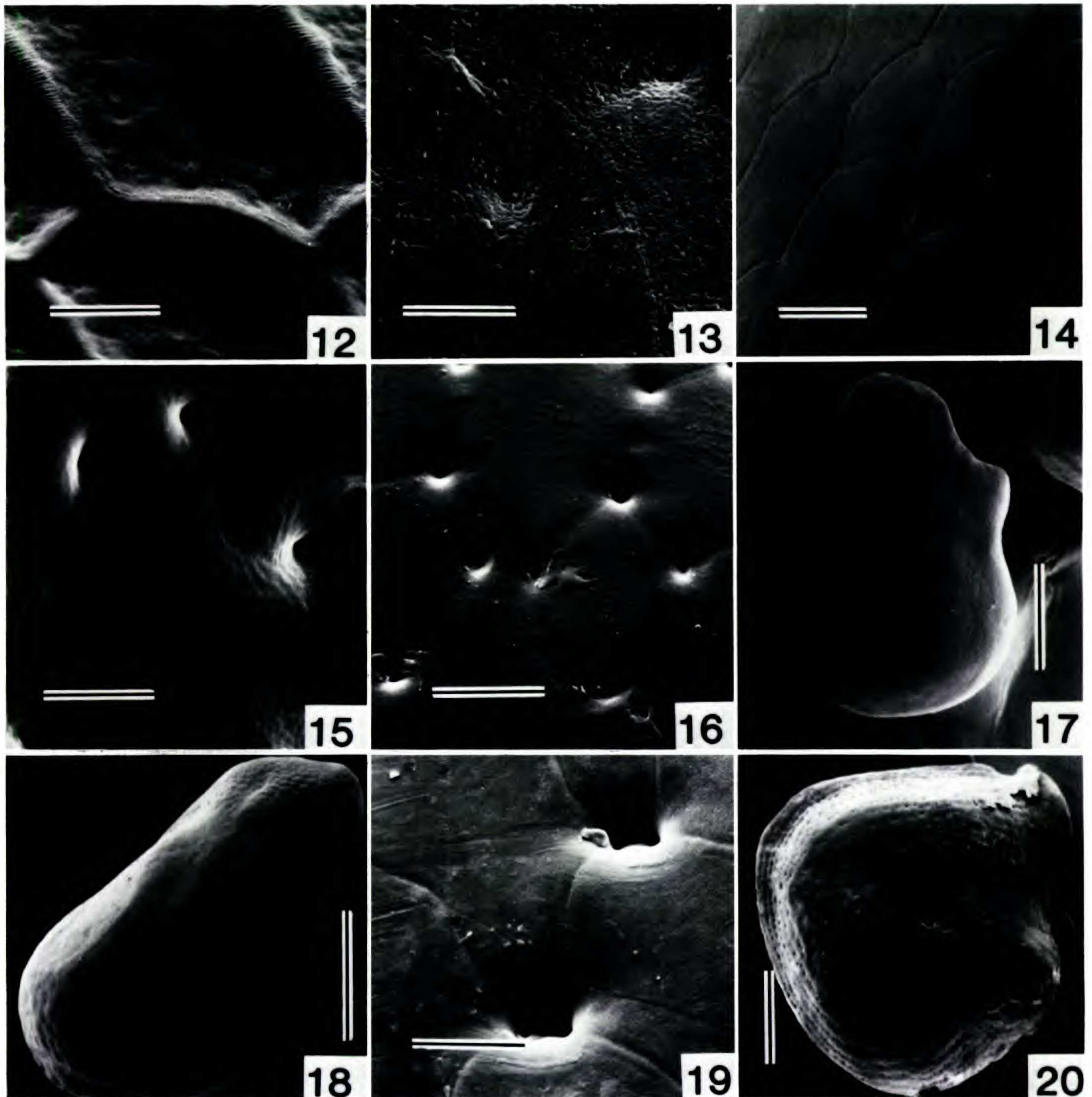
Morphological distinctiveness of seeds, fruits, and stem of *P. hollianus* were reanalyzed when Unger et al. (1980) surveyed tetrahydroisoquinoline alkaloids in eight species of Pachycereinae but reported none in *P. hollianus*, whereas the other species of *Pachycereus* had many important alkaloids. Consequently, Gibson (1982) recommended that the old name, *Lemaireocereus hollianus*, be used to recognize a monotypic genus of Pachycereinae and presumably a sister taxon of *Pachycereus*.

Stem triterpenes. In Gibson and Horak (1978), stem triterpene data obtained earlier by Djerassi played a key role in the reorganization of the species into subtribes, and the distribution of triterpene skeletons was used to evaluate the intrageneric relationships of species in Stenocereinae. However, plant chemotaxonomists should compare taxa by using the glycosidic forms of secondary compounds, the actual plant com-

pounds, because the glycosides have maximum information content (Giannasi, 1978; Crawford & Mabry, 1978; Stuessy & Crawford, 1983; Spencer & Siegler, 1985).

A fairly simplistic survey was made of triterpene chemistry of 20 available species of Stenocereinae and four other species of columnar cacti, first to determine whether they have abundant triterpenes and then to estimate the overall similarity of the glycosidic triterpenes of the species. Extractions were made in the field by grinding pieces of cortex with skin and spines of young, vigorous shoots in a blender with 95% ethanol. Each extract was filtered and concentrated in a flask evaporator to a thick syrup, and the syrup was partitioned between water, ethyl acetate, and ether to remove waxes. Triterpenes and carotenoids that appeared in the ethyl acetate fraction were chromatographed on silica gel thin-layer chromatographic plates in a variety of solvents, including 10:1, chloroform:methanol, 1:1, hexane:ethyl acetate, and 100:100:1, n-heptane:benzene:methanol. Compounds were detected with Lieberman-Burchard reagent and vanillin reagent and examined with UV light. From these extractions, a total of over 50 distinct compounds tested positive as triterpenes. These new phytochemical studies revealed abundant triterpenes in four species of Stenocereinae that had not been investigated by Djerassi, *S. kerberi*, *S. fricii* Sánchez Mejorada, *S. chrysocarpus* Sánchez Mejorada, and *S. standleyi*, and also from the plant called *Lemaireocereus thurberi* (Engelm.) Britt. & Rose var. *littoralis* (K. Brandeg.) Linds. We also detected large numbers of triterpenes in *Bergerocactus emoryi* and several triterpenes in *Lemaireocereus humilis* Britt. & Rose, but *Pterocereus gaumeri* (Britt. & Rose) MacDoug. & Miranda lacked triterpenes and *Mitrocereus fulviceps* (Weber) Backeb. ex Buxb. produced one equivocal band. Hence, the presence of abundant glycosidic triterpenes was verified as a good marker for Stenocereinae, because in the 25 species (out of 30) that have been tested, all possess abundant triterpenes. The presence of many, apparently different triterpenes in *Bergerocactus* needs intensive study.

Because samples provided were small, isolation and chemical identification of the glycosidic triterpenes were not attempted. Instead, a small set of intraspecific and interspecific comparisons was conducted to estimate the relative similarity of taxa within the subtribe. Three or four species were run simultaneously on each thin-layer chro-



FIGURES 12–20. Scanning electron photomicrographs of testa of Pachycereaeae. — 12. *Stenocereus alamosensis* (Coul.) Gibs. & Horak, *Gibson 3709* (RSA); testa is fairly smooth, but faint striae traverse the cell margins. Bar = 0.2 mm. — 13. *Stenocereus beneckeii* (Ehrenb.) Berg. & Buxb., *Gibson 3726* (RSA). Bar = 0.2 mm. — 14. *Pachycereus pringlei* (S. Wats.) Britt. & Rose, *Gibson 3629* (liquid-preserved voucher). Bar = 0.1 mm. — 15. *Pachycereus marginatus* (DC.) Britt. & Rose var. *gemmatus* (Zucc.) Bravo, *Gibson 3722* (liquid-preserved voucher); deep pits form at cell junctions. Bar = 0.2 mm. — 16. *Pachycereus weberi* (Coul.) Backeb., *Gibson 3721* (RSA). Bar = 0.1 mm. — 17. *Lophocereus schottii* (Engelm.) Britt. & Rose, *Gibson 3195* (ARIZ); seed with slightly convex cell walls and smooth cuticle. Bar = 1 mm. — 18. *Cephalocereus hoppenstedtii* (Weber) K. Schum., *Gibson 3741* (RSA); this seed has a fairly well-developed raphe. Bar = 1 mm. — 19. *Lemaireocereus hollianus* (Weber) Britt. & Rose, *Gibson 3735* (RSA). Bar = 0.2 mm. — 20. *Lemaireocereus hollianus*; same seed as Figure 19, showing that this has a different shape than other Pachycereaeae. Bar = 1 mm.

matographic plate, and the sequence of bands on each plate was then compared using color reagents in a qualitative way. The conclusions drawn from these tests are, of course, very crude for estimating phylogenetic relationships, but informative (Fig. 21).

1. The 14 species of *Stenocereus* tested shared a common pattern of triterpene glycosides.

2. *Stenocereus stellatus* and *S. treleasei* (Britt. & Rose) Backeb. were essentially the same, and *S. stellatus* was also very similar to *S. gummosus*.

3. *Stenocereus standleyi* and the two rathbunias, *S. kerberi* and *S. alamosensis*, seemed to be identical in triterpenes. These three species were examined more closely with trial separation performed on a silica gel column using an ascending polar solvent system. Each specimen had 30 bands, which all appeared to be the same. This group of three species was most similar to the *S. stellatus* group. The two populations of *S. alamosensis* examined were identical.

4. The nine taxa tested that have glandular areolar trichomes, e.g., *S. thurberi* and *S. queretaroensis* (Weber) Britt. & Rose, were more similar to each other than they were to the previous two groups.

5. Within the taxon with glandular areolar trichomes, there were two groups, one with columnar cacti centered in Nueva Galicia (*S. fricii* to *S. chrysocarpus*) and another that reaches to the Sonoran Desert (*S. thurberi* and relatives).

6. Triterpene glycosides of *S. thurberi* appeared to be identical to those of "*Lemaireocereus thurberi* var. *littoralis*," which has been treated either as a variety of organ pipe cactus or a distinct species but does not yet have a *Stenocereus* name.

7. Two species, *S. eruca* (Brandeg.) Gibson & Horak and *S. dumortieri* (Scheidweil.) Buxb., had a number of unusual triterpenes, and decisions on these could not be made for placing them with any of the species groups.

8. The two species of *Polaskia* had relatively few, simple, and similar triterpene glycosides.

9. Both *Escontria chiotilla* (Weber) Rose and the three species of *Myrtillocactus* differed markedly from and were more complex than *Polaskia*.

10. *Escontria*, *Polaskia*, and *Myrtillocactus* shared some compounds with *Stenocereus*.

The results yielded no real taxonomic applications, but they should be compared with earlier statements on the presumed relationships of these species. The close similarity of the three species in the rathbunia alliance based on 30 triterpene bands lends support to elimination of *Rathbunia*, which was previously argued on morphological grounds. Next, according to these data, *S. gummosus* is most closely related to *S. stellatus*. Gibson and Horak (1978) had presumed that the sister taxon of *S. gummosus* (Engelm.) Gibson & Horak was *S. fricii*, based solely on examination of literature accounts. Another northern cactus, *S. thurberi*, does appear to be related to *S. quevedonis* (G. Ortega) Buxb., as suggested in Gibson and Horak (1978), but *S. beneckeii* should

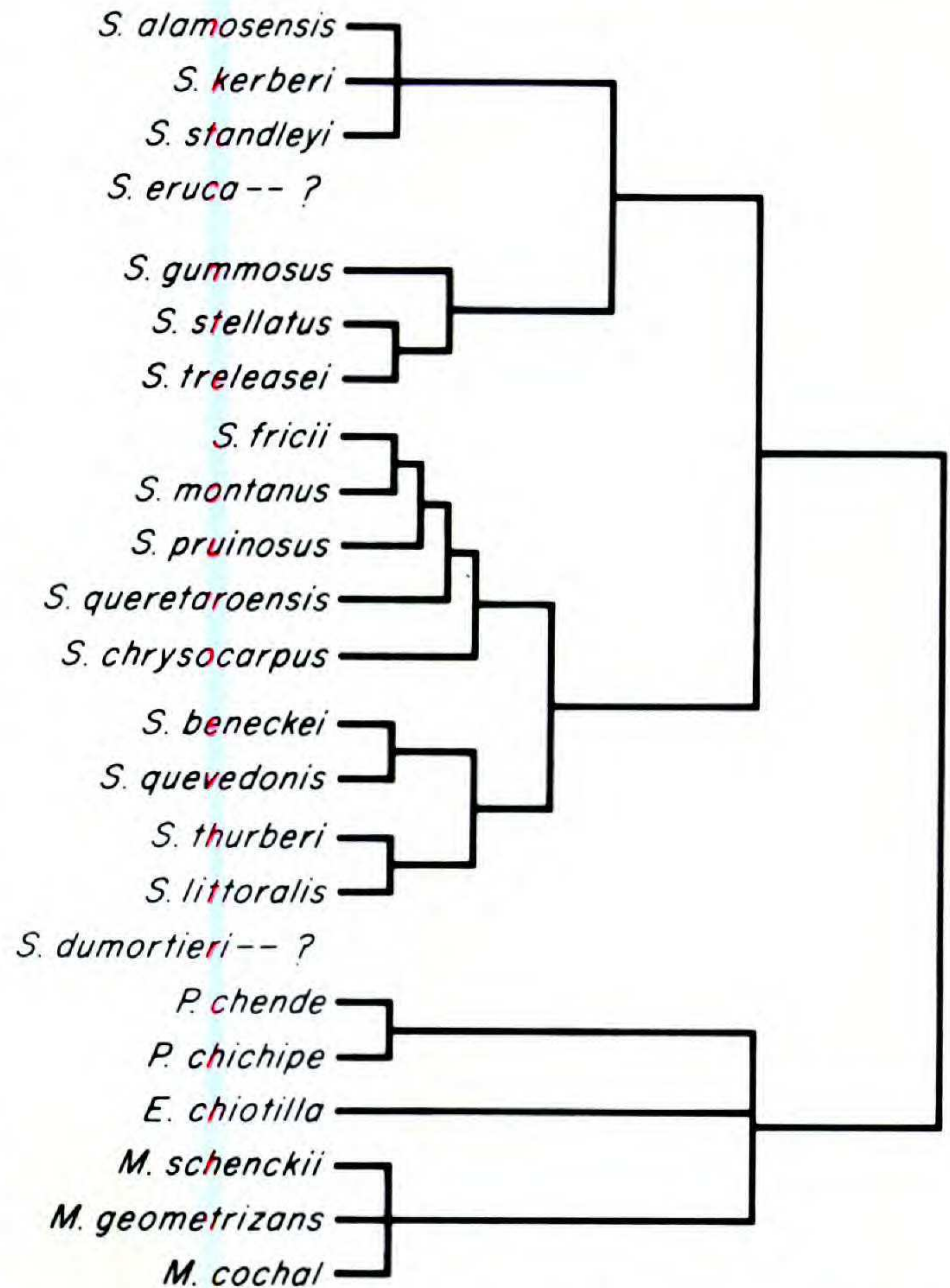


FIGURE 21. Crude dendrogram that shows the qualitative similarities of glycosidic triterpenes found in 21 taxa of Stenocereinae. *S.* = *Stenocereus*, *P.* = *Polaskia*, *E.* = *Escontria*, *M.* = *Myrtillocactus*.

be considered as a member of this group. *Stenocereus eruca* has always been treated as a derivative of *S. gummosus*, because both have similar flowers, fruits, and spines and occur in Baja California. This may be correct, but additional studies are needed to explain why the stem chemistry of these two species is so different.

Stem flavonoids. Research on flavonoids in cacti has been overshadowed by that on betalain pigments, which are unique in the Centrospermae (Mabry, 1976). Recently, several authors have reviewed data on flavonoids from cactus flowers and stems (Clark & Parfitt, 1980; Burret et al., 1981; Miller & Bohm, 1982), but flavonoids had not been studied in Pachycereeae.

To determine the relative value of flavonoids for phylogenetic models of Pachycereeae, a very simplistic survey was conducted using the same ethanol extractions obtained for triterpene analysis. A survey of flavonoids was conducted using two-dimensional paper chromatography; and R_f values and standard indicator sprays viewed under UV light were used to analyze the results. Surprisingly, over 200 distinct flavonoids were

TABLE 2. Columnar cacti tested for alkaloids from ethanol or CHCl₃ extracts. All species except "*Lemaireocereus humilis*," sometimes called *Armatocereus humilis*, are currently classified in tribe Pachycereeae. Authorities for all taxa appear in Gibson and Horak (1978).

Taxon	Voucher or Source	Wt. of Dry Plant Material/g	Wt. of Alcoholic/Chloroform Extract	Wt. of Fractions/mg		
				B	A	C
Ethanol Extracts						
1. <i>Backebergia militaris</i>	<i>Gibson 3717 (RSA)</i>	19.7	4.7	85.0	246.0	290.0
2. <i>Cephalocereus chrysacanthus</i>	<i>Gibson 3743 (RSA)</i>	19.7	2.3	125.0	32.5	99.5
3. <i>C. collinsii</i>	<i>Gibson 3742 (RSA)</i>	22.0	2.89	89.0	42.0	95.0
4. <i>C. hoppenstedtii</i>	<i>Gibson 3741 (RSA)</i>	44.6	3.1	184.0	8.0	158.5
5. <i>C. purpusii</i>	<i>Gibson 3710 (RSA)</i>	15.0	3.8	99.0	200.0	199.5
6. <i>C. senilis</i>	<i>Gibson 3750 (RSA)</i>	17.8	2.0	120.0	9.0	97.5
7. <i>C. totolapensis</i>	<i>Gibson 3740 (RSA)</i>	26.3	2.4	129.0	7.0	77.5
8. <i>Escontria chiotilla</i>	<i>Gibson 3751 (RSA)</i>	28.7	12.6	341.0	78.0	300.0
9. <i>Lemaireocereus hollianus</i>	<i>Gibson 3735 (RSA)</i>	6.7	0.9	30.0	39.0	310.0
10. <i>Mitrocereus fulviceps</i>	<i>Gibson 3744 (RSA)</i>	11.5	1.5	180.0	8.0	115.0
11. <i>Neobuxbaumia macrocephala</i>	<i>Gibson 3745 (RSA)</i>	36.2	6.1	247.0	7.0	92.5
12. <i>N. mezcalaensis</i>	<i>Gibson 3725 (RSA)</i>	56.5	3.4	246.0	12.5	140.5
13. <i>N. mezcalaensis</i>	<i>Gibson 3756 (RSA)</i>	23.8	3.7	98.5	5.0	94.0
14. <i>N. tetetzo</i>	<i>Gibson 3737 (RSA)</i>	29.5	2.4	201.5	7.0	32.5
15. <i>Pachycereus grandis</i>	<i>Gibson 3749 (RSA)</i>	21.4	1.2	403.0	45.3	167.0
16. <i>P. marginatus marginatus</i>	<i>Gibson 3755 (RSA)</i>	6.2	2.1	90.0	150.0	196.0
17. <i>P. pecten-aboriginum</i>	<i>Gibson 3748 (RSA)</i>	15.9	1.3	128.5	44.0	93.0
18. <i>P. weberi</i>	<i>Gibson 3728 (RSA)</i>	15.1	1.2	72.6	84.5	173.0
19. <i>P. weberi</i>	<i>Gibson 3721 (RSA)</i>	15.9	1.2	173.0	29.0	180.5
20. <i>Stenocereus dumortieri</i>	<i>Gibson 3727 (RSA)</i>	22.3	11.0	85.0	67.0	320.0
CHCl₃ Extracts						
21. <i>Lemaireocereus humilis</i>	<i>Gibson 3183 (ARIZ)</i>	10.0	0.25	21.0	13.5	14.5
22. <i>Neobuxbaumia polylopha</i>	Huntington Botanical Garden	15.0	1.5	9.0	8.0	4.5
23. <i>Pachycereus grandis</i>	<i>Gibson 3749 (RSA)</i>	15.0	0.20	19.5	11.0	11.0
24. <i>P. pecten-aboriginum</i>	40 km south of Ciudad Obregon, Sonora, Mexico	20.0	0.70	55.5	105.5	87.5
25. <i>Polaskia chende</i>	<i>Gibson 3180 (ARIZ)</i>	5.0	1.75	submitted for mass spec./mass spec. analysis		
26. <i>Pterocereus gaumeri</i>	Huntington Botanical Garden	6.96	0.20	24.0	24.0	31.0
27. <i>Stenocereus beneckeii</i>	Huntington Botanical Garden	5.0	0.13	submitted for mass spec./mass spec. analysis		
28. <i>S. stellatus</i>	Huntington Botanical Garden	5.0	0.18	submitted for mass spec./mass spec. analysis		

detected from the 24 species, and on a chromatograph of *Stenocereus thurberi*, there were at least 70 distinct spots. Most specimens had more than 40 distinct phenolic compounds. This ap-

parent diversity is remarkable because the studies of other Cactaceae have included few reports of flavonoids in stem tissues. No attempt was made to identify these phenolic compounds be-

Extraction and Identification of Alkaloids
from Cactus Plants by Thin Layer Chromatography

1) Extraction Procedure for Alcoholic Extracts. Scheme I

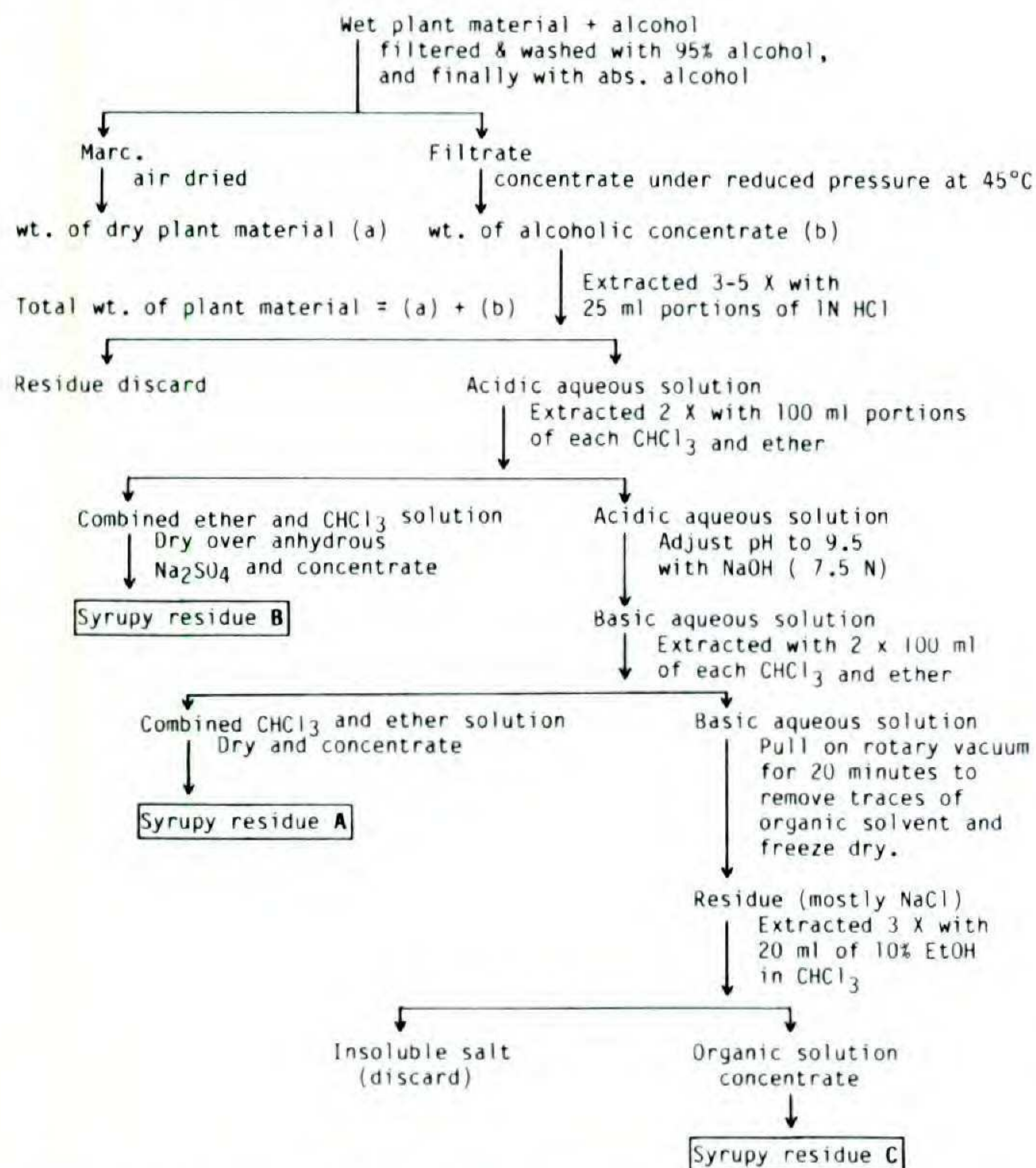


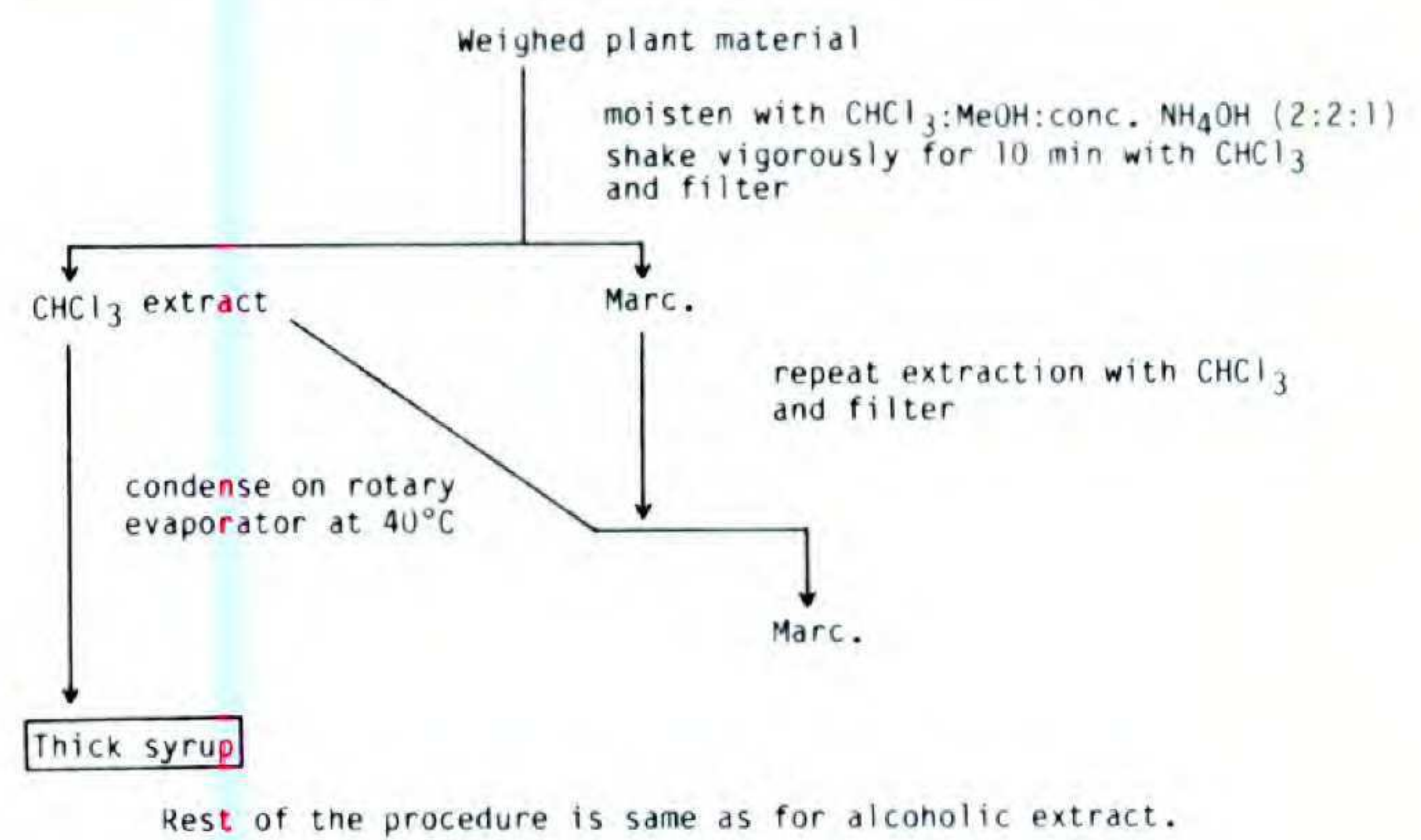
FIGURE 22. Flow chart of the extraction and identification of alkaloids from cactus stems by thin-layer chromatography using ethanolic extracts (Scheme I).

cause there were so many and because the samples and sample sizes were very small. Nevertheless, comparisons among *S. standleyi*, *S. kerberi*, and *S. alamosensis* revealed 41 visually identical spots, many of which were not present in other species. This observation reinforces the previous statement based on the visual similarities of 30 triterpenes, and these and morphological evidence suggest that these three species are not only closely related but also fairly recent segregates.

Stem alkaloids. Prior to 1977 alkaloids had been detected in seven species of Pachycereae (Djerassi et al., 1953, 1954, 1956, 1958, 1972; Agurell, 1969; Bruhn et al., 1970; Bruhn, 1971; Bruhn & Lindgren, 1976; Bruhn & Lundström, 1976). Most research had concentrated on these unique tetrahydroisoquinoline alkaloids.

The phylogenetic hypothesis of Gibson and Horak (1978) placed all known alkaloid-bearing species of this tribe in Pachycereinae, and this model inferred that other alkaloid-bearing species should occur in that subtribe. The model was immediately tested for this prediction, and investigators found abundant and even new alkaloids in the chemically unknown *Backebergia militaris* (Audot) Bravo ex Sánchez Mejorada

2) Extraction Procedure for Powdered Plant Material. Scheme II



3) TLC Systems Used (silica gel plates)

- | | |
|---|-----------|
| a) Ether:Acetone:MeOH:NH ₄ OH (conc.) | 5:3:3:0.5 |
| b) Ether:MeOH:NH ₄ OH (conc.) | 4:1.5:0.5 |
| c) EtOH:CHCl ₃ :NH ₄ OH (conc.) | 4:3:0.5 |
| d) Ethyl acetate:MeOH:NH ₄ OH (conc.) | 8:1.5:0.5 |
| e) CHCl ₃ :Acetone:Diethylamine | 5:4:1 |

4) Spray Reagents Used

- UV light (plates have fluorescent indicator)
- Fluram (Fluorescamine) 0.02% in acetone
- Tetrazotized benzidine reagent
- Iodoplatinate

FIGURE 23. Flow chart of the extraction and identification of alkaloids from cactus stems by thin layer chromatography using powdered materials obtained from fresh plants (Scheme II).

(Mata & McLaughlin, 1980a; Pummangura & McLaughlin, 1981) as well as in species that had not been examined very closely (Mata & McLaughlin, 1979, 1980b, 1980c). Alkaloids known from Pachycereinae before 1981 are listed in Mata and McLaughlin (1982).

Extractions were made in the field for 16 species of Pachycereinae and two species of Stenocereinae (Table 2) by grinding pieces of cortex with skin and spine of young, vigorous shoots in a blender with 95% ethanol. These were then analyzed using the isolation procedure outlined in Scheme I of Figure 22, and all recovered fractions (A-C) were tested for alkaloids. In addition, chloroform extractions were made from powdered (freeze-dried fresh) stems of nine species (Table 2) using Scheme II in Figure 23. Methods used for identifying the alkaloids have been published previously (Ranieri & McLaughlin, 1976).

Table 3 lists the alkaloids identified by thin-layer chromatography from these samples, and Figures 24 and 25 show the chemical structure of each alkaloid. This survey demonstrated that alkaloids are present in some species of *Cephalocereus*, *Neobuxbaumia mezcalaensis* (Bravo) Buxb., and *Pachycereus grandis* Rose, which had not previously been tested. However, the survey made two other important findings. First, it showed that not all Pachycereinae have alkaloids, because alkaloids could not be detected in

TABLE 3. Alkaloids identified from columnar cacti (Table 2) by Bajaj and McLaughlin using thin-layer chromatography. Each alkaloid cochromatographed and gave identical visualization reactions with reference alkaloids in all (at least three) solvent systems tested.

Species	Alkaloids Identified by TLC	Fraction/ A/B/C
1. <i>Backebergia militaris</i>	1) Backebergine (traces) 2) Dehydroheliamine 3) 3,4-dimethoxy PEA 4) Lemaireocereine (traces) 5) N,N-dimethyl-3,4-dimethoxy PEA 6) Heliamine 7) N-methyl-3,4-dimethoxy PEA	A A A/C A A A A
2. <i>Cephalocereus chrysacanthus</i>	1) N,N-dimethyl-3,4-dimethoxy PEA 2) N-methyl-3,4-dimethoxy PEA	A A
3. <i>Cephalocereus collinsii</i>	1) N,N-dimethyl-3,4-dimethoxy PEA 2) N-methyl-3,4-dimethoxy PEA	A A
4. <i>Cephalocereus hoppenstedtii</i>	1) N-methyl-3,4-dimethoxy PEA (traces)	A
5. <i>Cephalocereus purpusii</i>	1) Tyramine 2) N-methyl-3,4-dimethoxy PEA 3) Dehydroheliamine 4) three unidentified alkaloids	A A A A/C
6. <i>Cephalocereus senilis</i>	No alkaloid	
7. <i>Cephalocereus totolapensis</i>	No alkaloid	
8. <i>Escontria chiotilla</i>	One unidentified polar secondary alkaloid	A/C
9. <i>Lemaireocereus hollianus</i>	1) N,N-dimethyl-3,4-dimethoxy PEA (traces) 2) N-methyl-3,4-dimethoxy PEA (traces) 3) 3,4-dimethoxy PEA 4) 3-methoxytyramine 5) N-methoxy-3-methoxytyramine	A A A C C
10. <i>Mitrocereus fulviceps</i>	No alkaloid	
11. <i>Neobuxbaumia macrocephala</i>	No alkaloid	
12. <i>N. mezcalaensis</i>	One unidentified alkaloid (traces)	
13. <i>N. mezcalaensis</i>	1) Heliamine (traces)	C
14. <i>N. tetetzo</i>	No alkaloid	
15. <i>Pachycereus grandis</i>	No alkaloid	
16. <i>Pachycereus marginatus marginatus</i>	1) Pilocereine 2-3 unidentified alkaloids	A A
17. <i>Pachycereus pecten-aboriginum</i>	1) Heliamine 2) Salsoline 3) 3,4-dimethoxy PEA (traces) 4) 3-methoxytyramine	A A A A
18. <i>P. weberi</i>	1) Dehydroheliamine (conc.) 2) Tehuanine (conc.) 3) Pellotine (traces) 4) Lemaireocereine (traces) 5) Weberidine (traces) 6) Nortehuanine 7) Anhalonidine 8) Heliamine	A/C A A A A A A/C A/C
19. <i>P. weberi</i>	1) Dehydroheliamine 2) Tehuanine 3) 3-methoxytyramine 4) Tyramine (traces)	A A A/C C
20. <i>Stenocereus dumortieri</i>	Traces of two unidentified alkaloids	A
21. <i>Lemaireocereus humilis</i>	No alkaloid	

TABLE 3. Continued.

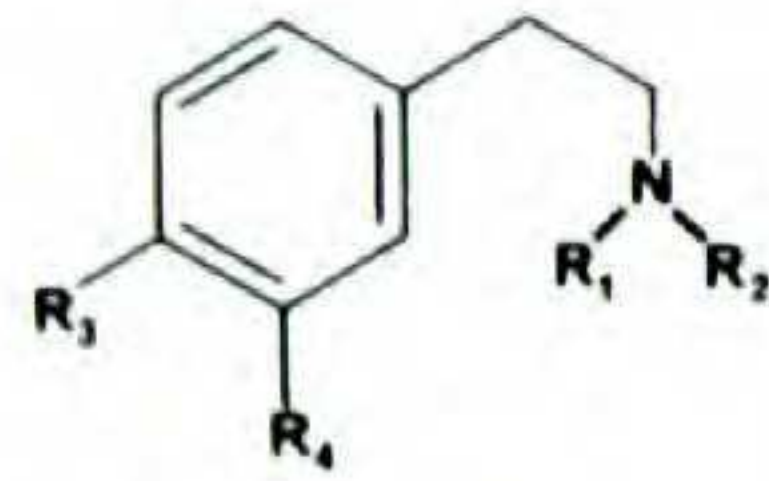
Species	Alkaloids Identified by TLC	Fraction/ A/B/C
22. <i>Neobuxbaumia polylopha</i>	No alkaloid	
23. <i>Pachycereus grandis</i>	1) Tehuanine	A
	2) O-methylpellotine	A
	3) N-methylheliamine (traces)	A
	4) Carnegine	A
24. <i>P. pecten-aboriginum</i>	1) Tehuanine (traces)	A
	2) O-methylpellotine	B/A
	3) Carnegine (conc.)	B/A/C
	Two unidentified alkaloids	B/A
25. <i>Polaskia chende</i>	One primary alkaloid	A/C
26. <i>Pterocereus gaumeri</i>	1) Deglucopterocereine	A/C
	Two unidentified tertiary alkaloids (high conc.)	A/C
27. <i>Stenocereus beneckeii</i>	One primary alkaloid	A/C
28. <i>S. stellatus</i>	Three primary alkaloids	A/C

Mitrocereus fulviceps, four species of *Neobuxbaumia*, and several species of *Cephalocereus*, including the type, *C. senilis* (Haw.) Pfeiff. Second, alkaloids were discovered in *Stenocereinae*. To date, primary alkaloids have been detected in *Polaskia chende*, *Stenocereus beneckeii*, *S. dumortieri*, *S. stellatus*, and *S. treleasei*; whereas *Escontria chiotilla* from Puebla contained an unidentified secondary alkaloid. Moreover, *S. eruca* showed a positive test with commonly used alkaloid indicators.

The tetrahydroisoquinoline alkaloids have been found in all species of *Pachycereus*, *Lophocereus*, *Backebergia*, and *Carnegiea*, in *Pterocereus gaumeri*, two species of *Cephalocereus*, and *Neobuxbaumia mezcalaensis*, whereas the simpler alkaloids of tyramine and phenethylamine occur in most of these same species as well as in *Lemnaireocereus hollianus* and numerous species of *Cephalocereus* (Mata & McLaughlin, 1982). The high diversity of tetrahydroisoquinoline alkaloids (about 25 different compounds) in this group is in sharp contrast to their poor representation in other cactus taxa; and the occurrence of these secondary metabolites in the genera *Pachycereus*, *Lophocereus*, and *Backebergia* is a fairly good indicator that these genera are closely related, especially because these taxa possess other synapomorphic morphological and anatomical features. In addition, fresh stems of all five species of *Pachycereus* and *Backebergia* turn red and then blacken rapidly when they are cut, which in *P. weberi* was shown to be caused by the hydrolysis of the glucoside lemairin (Mata & McLaughlin, 1980d). Of the species rich in tetrahydroisoquin-

olines, *Lophocereus* and *P. marginatus* are chemically very similar and distinct from the rest of the species, which frequently share the same compounds. In contrast, *Carnegiea*, which superficially appears to share many alkaloids with *Pachycereus*, can be distinguished from the other species because it has different isomers of tetrahydroisoquinolines, suggesting that a different biosynthetic pathway may be involved (Unger et al., 1980); also, cut stems of *Carnegiea* blacken very slowly. *Pterocereus* has two unique alkaloids; however, this observation cannot be used as evidence for or against inclusion of this genus in *Pachycereinae*.

The abundance of primary alkaloids in *Pachycereinae* is an unreliable feature for analyzing relationships within the *Pachycereinae* because these are not only absent in some of the species but also are widespread compounds in all three subfamilies of Cactaceae, e.g., mescaline, the peyote hallucinogen (Doetsch et al., 1980). Primary alkaloids have now been discovered in six species of *Cephalocereus* s.l., including *C. hoppenstedtii* but not in the very closely related type species, *C. senilis*, and not in *C. totolapensis*, which has been classified as the genus *Neodawsonia* Backeb. Because *Mitrocereus fulviceps* and the species of *Neobuxbaumia* are not rich in stem alkaloids and share the pattern of calcium oxalate crystals in the skin, all of these *Pachycereinae* species that lack abundant tetrahydroisoquinoline alkaloids appear to be a clade, separate from the clade of *Lophocereus*, *Backebergia*, and *Pachycereus*. Placement of the alkaloid-rich *Carnegiea* and of *Lemnaireocereus hollianus* is still



$R_1, R_2, R_4 = H; R_3 = OH$: tyramine

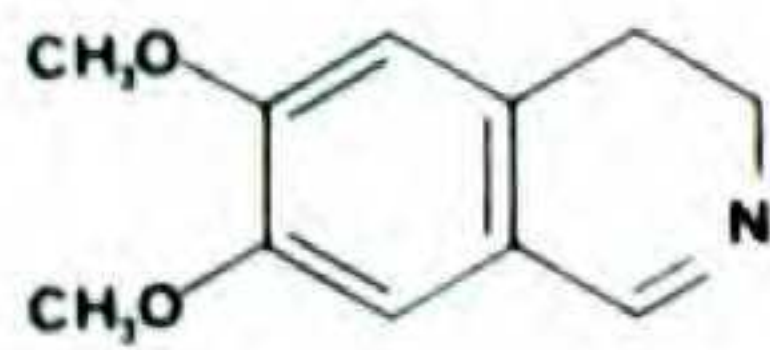
$R_1, R_2 = H; R_3, R_4 = CH_3O$: 3,4-dimethoxy PEA

$R_1 = CH_3; R_2 = H; R_3, R_4 = CH_3O$: N-methyl-3,4-dimethoxy PEA

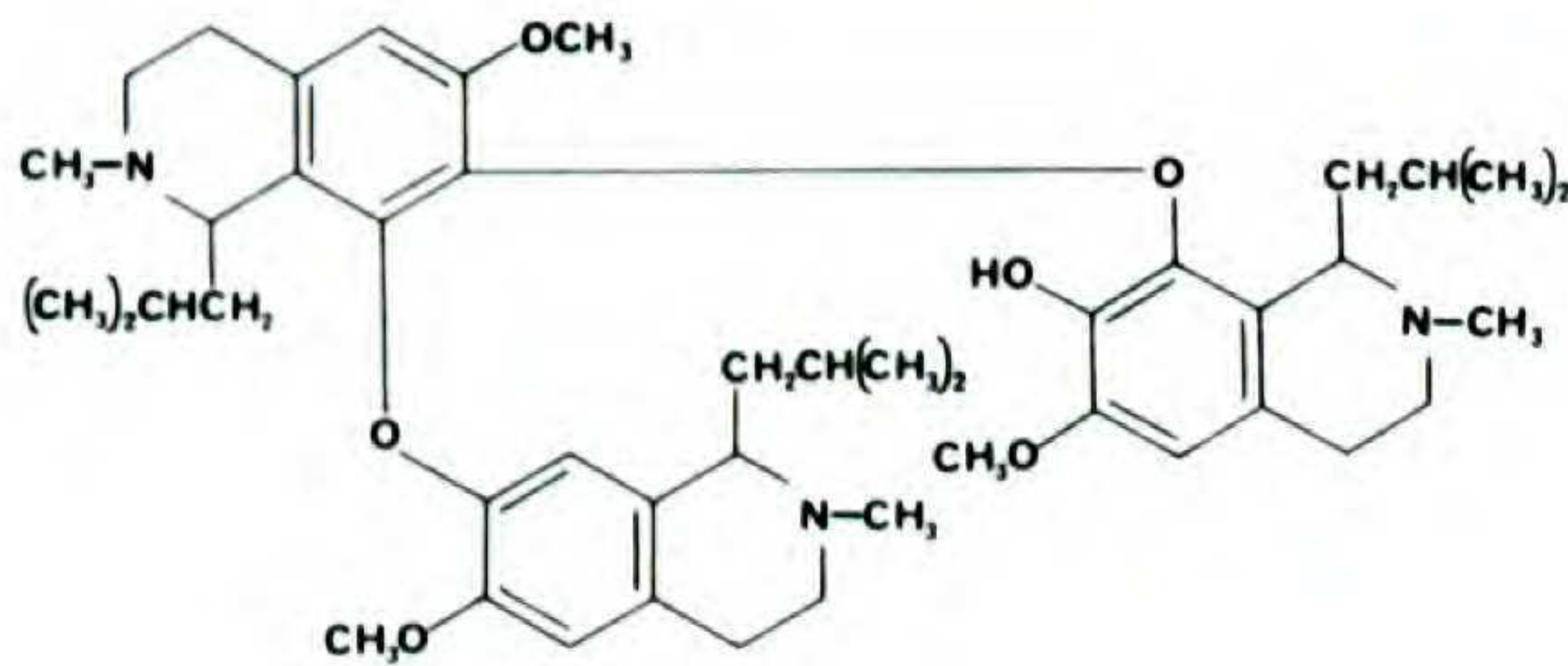
$R_1, R_2 = CH_3; R_3, R_4 = CH_3O$: N,N-dimethyl-3,4-dimethoxy PEA

$R_1, R_2 = H; R_3 = OH; R_4 = OCH_3$: 3-methoxytyramine

$R_1 = H; R_2 = CH_3; R_3 = OH; R_4 = OCH_3$: N-methyl-3-methoxytyramine



dehydroheliamine



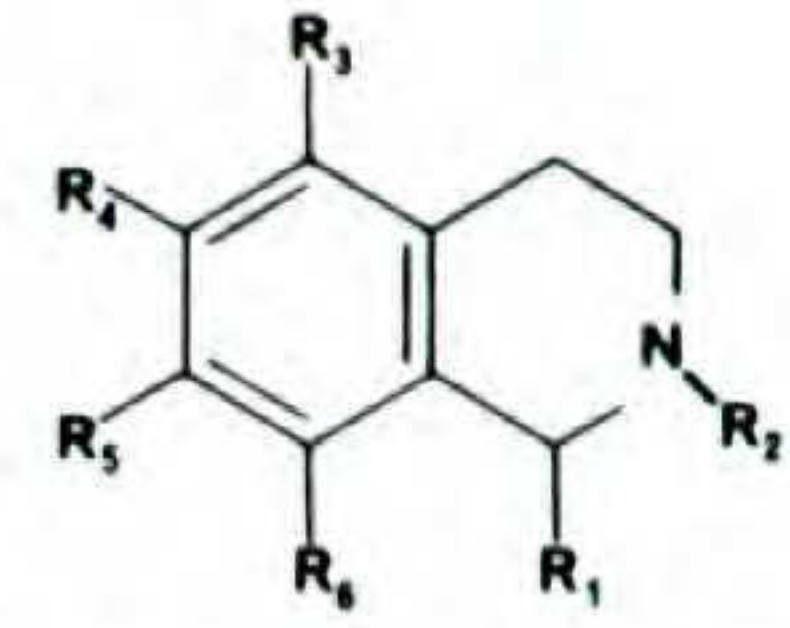
pilocerine

FIGURE 24. Alkaloids isolated from columnar cactus stems (Tables 2 and 3).

problematic, although on morphological grounds *Carnegiea* is most similar to *Neobuxbaumia euphorbioides* (Haw.) Buxb., which appears to lack alkaloids entirely.

Phylogenetic conclusions on Pachycereeae. The theme of this paper has been that systematic treatments of cacti have been in a constant state of flux since Linnaeus first assigned them Latin binomials. With each additional data set, interspecific relationships have been reanalyzed and taxa readjusted to achieve a more parsimonious phylogenetic model. Instead of relying only on gross, external morphological features to reconstruct phylogenies, workers have had to use more subtle or hidden synapomorphic features, such as characters of stem anatomy, seed ultrastructure, areolar and funicular pigmentation, and stem chemistry, to uncover genealogical relationships of the species. Phylogenetic hypotheses generated by combining new and subtle parameters with traditional and conspicuous features are producing a new classification of the large columnar cacti of Mexico, which can be used to study patterns of speciation in the Pachycereeae and to stabilize nomenclature.

Some aspects of the phylogenetic studies of Pachycereeae are still unresolved, in part because morphological, anatomical, and chemical data



$R_1 = CH_3; R_2 = H; R_3 = H; R_4 = OH; R_5 = CH_3O; R_6 = H$: salsoline

$R_1, R_2 = H; R_3 = H; R_4, R_5 = CH_3O; R_6 = H$: heliamine

$R_1, R_2, R_3, R_4 = H; R_5, R_6 = CH_3O$: lemaireocereine

$R_1 = H; R_2 = CH_3; R_3, R_4, R_5 = CH_3O; R_6 = H$: tehuanine

$R_1, R_2 = CH_3; R_3 = H; R_4, R_5 = CH_3O; R_6 = OH$: pellotine

$R_1, R_2, R_3, R_4 = H; R_5 = CH_3O; R_6 = H$: weberidine

$R_1, R_2 = H; R_3, R_4, R_5 = CH_3O; R_6 = H$: nor-tehuanine

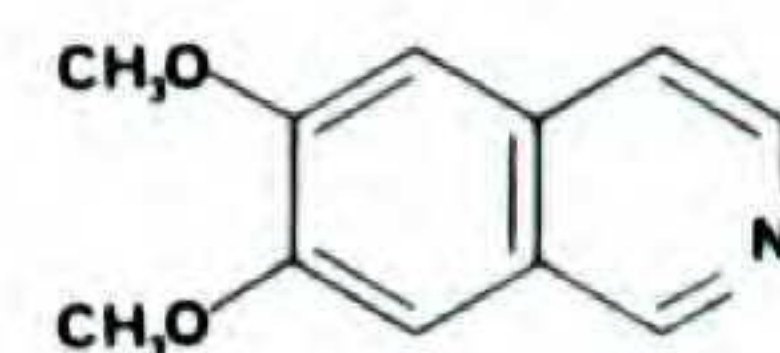
$R_1 = CH_3; R_2, R_3 = H; R_4, R_5 = CH_3O; R_6 = OH$: anhalonidine

$R_1, R_2 = CH_3; R_3 = H; R_4, R_5, R_6 = CH_3O$: O-methyl-pellotine

$R_1 = H; R_2 = CH_3; R_3 = H; R_4, R_5 = CH_3O; R_6 = H$: N-methylpellotine

$R_1, R_2 = CH_3; R_3 = H; R_4, R_5 = CH_3O; R_6 = H$: carnegine

$R_1 = CH_2OH; R_2 = CH_3; R_3 = OH; R_4, R_5 = CH_3O; R_6 = H$: deglucopterocereine



backebergine

FIGURE 25. Alkaloids isolated from columnar cactus stems (Tables 2 and 3).

are incomplete on species residing in southernmost Mexico, and in part because we seem to be running out of "easy" synapomorphies to use in discerning cladogenesis in some of the species groups. For example, to use triterpene and flavonoid data for phylogenetic reconstruction of Stenocereinae, a massive project would be needed to identify each glycosidic compound in sample populations of every species, and this project is not a trivial one because these species have 50–100 distinct compounds per sample.

Tribe Pachycereeae has not yet been defined as a true monophyletic clade, because there is no way to determine at this time with our insufficient data base whether taxa currently classified in other tribes should be brought into Pachycereeae and whether other taxa, such as some of the remnants of *Lemaireocereus*, are part of Pachycereeae. For example, one current problem is *L. aragonii* Britt. & Rose, which grows in dry tropical deciduous forest and disturbed habitats in western Costa Rica. Like *Pachycereus marginatus*, this species can be used as a living fence because its young, unbranched stems root very easily; in addition, this Costa Rican taxon does not appear to produce flowers and fruits very often. Britton and Rose (1919–1923) presented a very incomplete diagnosis of *L. aragonii*, but they were impressed by the wax chevrons produced on young stems marking growth intervals. The seeds of this species were described as shiny,

black, and 3 mm long, features not expected in Stenocereinae but more similar to *Pachycereus*. However, stem materials collected in Costa Rica by M. E. Mathias were examined and found to have none of the characteristic features of either taxon, and they do not blacken when cut. If *L. aragonii* is a species of *Armatocereus*, which it might be, then extensive studies of that genus are required, and then a study of columnar forms must be extended to northern South America. Moreover, this species is the type of *Marshallocereus* Backeb., which included *Stenocereus thurberi*, so additional nomenclatural problems may have to be resolved.

Searching for outgroups to produce a convincing model of Pachycereae is also not a trivial matter. The normal procedure for studying phylogenetic systematics is to know the limits of the taxon and probable outgroups *before* analyzing infrataxon relationships. Certainly, this cannot be done in cacti without strongly biasing analyses, and it is safer to start reconstructing the phylogenies of tight species groups and work gradually to higher taxonomic levels. Using Stenocereinae as a model, we can see how this can be accomplished, assuming that all species have been included and making informed decisions on where generic lines should be drawn. For example, in Stenocereinae, *Escontria*, *Myrtillocactus*, *Polaskia*, and *Stenocereus* are defensible genera because they are each sharply defined by several to many structural and chemical synapomorphies, and each is as distinct as many well-defined genera in other tribes of Cactoideae. For these same reasons, it makes no sense to continue to use the name *Cereus* for any native columnar cactus from Mexico, because *Cereus* s.s. is as distinctive in its own way and has not been ancestral to either Stenocereinae or Pachycereinae.

The problems of developing a parsimonious phylogenetic model of cacti are not insurmountable if workers begin to abandon earlier treatments and reanalyze synapomorphies. An example of this is the epiphytes, which have been another longstanding systematic conundrum. The most recent generic classification of cacti by Hunt (1967) placed all epiphytic genera in one tribe, Hylocereae Buxb., which included the terrestrial genus *Selenicereus* Britt. & Rose. This treatment is unsatisfactory for three important reasons. First, the primarily South American rhipsalid genera appear to be most closely related to *Corryocactus* Britt. & Rose (incl. *Erdisia* Britt.

& Rose; tribe Notocactae Buxb.), and cannot be related to the ribbed epiphytes of Mesoamerica. Second, even among the epiphytic genera centered around Mesoamerica, there seem to be three clades, and each of these epiphytic lineages is most closely related to a different terrestrial genus, *Selenicereus*, *Acanthocereus* (A. Berger) Britt. & Rose, or *Nyctocereus* (A. Berger) Britt. & Rose. Therefore, epiphytism has apparently evolved independently in the family at least four times. Finally, if epiphytes have evolved repeatedly from terrestrial forms, then a phylogenetic classification must place terrestrial and epiphytic sister groups in the same taxon. This is the future direction that cactus systematics must take so that the evolutionary history of this family can be properly studied.

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